

FUTURE POPULATION TRENDS AND DRIVERS OF CHANGE FOR ALEXANDER
ARCHIPELAGO WOLVES ON AND NEAR PRINCE OF WALES ISLAND,
ALASKA

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ABSTRACT

The Alexander Archipelago wolf, inhabiting the coastal temperate rainforest of North America from British Columbia to southeastern Alaska, was recently petitioned for protection under the U.S. Endangered Species Act. Concerns about habitat alteration from industrial timber harvest and subsequent declines in prey (deer), increased human-caused mortality, and climate change were presented as the basis for the listing. To evaluate how these factors will likely affect future trends in abundance for Alexander Archipelago wolves and deer, we constructed a model linking wolf and deer population dynamics to environmental conditions and management regulations. We restricted our model to Prince of Wales and outlying islands, because this area is partially isolated, is the focus of timber harvest in the region, and has the most empirical data available for model parameterization. We examined the effects of timber harvest (past and future), winter severity, wolf harvest regulations, and roads, which affect deer and wolf harvest, on population dynamics of deer and wolves. Combining these factors, 6 future scenarios were developed by a panel of experts, and subsequently evaluated using the model. The ecological backdrop of this study is that high rates of logging during the 1970's and 1980's, and the lag in time over which habitat values for deer subsequently decline due to forest succession, resulted in a significant downward trajectory in carrying capacity for deer during 1995 – 2015, with varying levels of decline continuing through 2035 under all scenarios. Across scenarios, we found that wolf populations persisted, but with declines of 5–20% in wolf abundance and 21–32% in deer abundance after 30 years, with variation produced primarily by changes in road density, and smaller contributions from vegetation scenarios, severe-winter frequency, and wolf harvest regulation. In addition, we found that wolf declines could be greater if wolves rely more heavily on deer in the future, for instance if salmon availability declines under future climate change.

Various wolf harvest regulations (0%, 20% and 30% caps on reported harvest of the fall wolf population) did not produce large differences in wolf abundance because the harvest caps were calculated at the population level, which were frequently not met with our modeling approach. The potential importance of unreported harvest in wolf population dynamics needs further acknowledgement and treatment. Changes in deer harvest produced large increases in deer and wolf abundance. Although we evaluated factors affecting wolf abundance individually, we encourage a holistic approach to management of this predator-prey system in an altered ecosystem.

KEYWORDS: Alaska; U.S. Endangered Species Act; Alexander Archipelago wolf; predator-prey interaction; population dynamics

INTRODUCTION

The coastal temperate rainforest of the Pacific Northwest of North America is a globally rare ecosystem, with an assembly of species found nowhere else in the world. Within this eco-region, timber harvest and associated development have altered the landscape considerably over the last century, especially in the last 50 years, resulting in a patchwork of even-aged forest stands, intersecting roads, and small human settlements. The majority of remaining old-growth temperate rainforest in the U.S. is found in southeastern Alaska, the northernmost extent of the coastal temperate rainforest ecosystem, which is the focus of both the timber industry and conservation efforts.

One of the most controversial species inhabiting the coastal temperate rainforest of southeastern Alaska is the Alexander Archipelago wolf (*Canis lupus ligoni*), although its

subspecific designation currently is being debated (e.g., Chambers et al. 2012; Cronin et al. 2015; Weckworth et al. 2015). Morphologically, it is smaller and darker, with coarser and shorter hair compared to continental gray wolves (Goldman 1944, Wood 1990). Genetically, coastal wolves in southeastern Alaska and British Columbia are distinct from continental populations (Shields 1995; Weckworth et al. 2005; Weckworth et al. 2010; Munoz-Fuentes et al. 2009; but see Cronin et al. 2015). Within this coastal region, wolves exhibit some genetic population structure, especially on POW where the population is partially isolated (Weckworth et al. 2005, Breed 2007, Cronin et al. 2015b). The debate regarding taxonomic classification of the Alexander Archipelago wolf largely stems from the lack of a universally accepted definition for subspecies (Haig et al. 2006) and the absence of a comprehensive morphological and genetic assessment of coastal wolves. We assumed that the subspecies designation is valid and refer to coastal wolves as the Alexander Archipelago wolf throughout this report.

This assumed subspecies of the gray wolf depends on Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) as a primary food source, and is consequently affected by timber harvest as deer populations respond to post-harvest forest succession (Figure 1). This trophic link from wolves to deer to timber harvest, along with high harvest of wolves in areas accessible by road and boat (Person and Russell 2008, Person and Logan 2012), has resulted in concern for the long-term viability of wolves in southeastern Alaska. A major population of Alexander Archipelago wolves, inhabiting Prince of Wales and outlying islands, has declined sharply in recent years (Alaska Department of Fish and Game 2015a), further heightening concern. In 1993, a petition was filed for protection of the Alexander Archipelago wolf under the Endangered Species Act (ESA), but ultimately the U.S. Fish and Wildlife Service (USFWS) determined that listing as threatened or endangered was not warranted (62 Federal Register 46710, September 4,

1997). In 2011, a petition was again filed for protection of the Alexander Archipelago wolf under the ESA, citing cascading effects of past and future timber harvest, high rates of wolf harvest, climate change, and inadequacy of existing regulatory mechanisms as primary threats (Center for Biological Diversity and Greenpeace 2011). The USFWS published a positive 90-day finding in the Federal Register in March 2014, indicating that the petition included substantial information suggesting that listing may be warranted (79 Federal Register 17993, March 31, 2014), and initiated a status review shortly thereafter. Per a court agreement, the USFWS must issue a 12-month finding on whether or not listing is warranted on or before December 31, 2015. As part of this process, we were charged with conducting a population analysis of wolves on Prince of Wales Island (POW), the largest island in the Alexander Archipelago, along with associated smaller islands, and this final report summarizes our results.

Like their continental counterparts, coastal wolves are opportunistic predators, although their diet includes a greater marine component. Wolves in the coastal temperate rainforest prey on diverse species including Pacific salmon (*Onchorhynchus* spp.), mountain goat (*Oreamnos americanus*), marine mammals (e.g., harbor seal [*Phoca vitulina*]), American beaver (*Castor canadensis*), and a variety of birds. Although the diet of coastal wolves is diverse, deer is the most important prey item. In southeastern Alaska, deer typically represent at least half of annual wolf diet and Pacific salmon account for upwards of 20% of the annual wolf diet (Szepanski et al. 1999, Person 2001), although during late summer and autumn when adult salmon enter rivers to spawn, salmon can be the dominant prey item (Darimont et al. 2008). The proportion of deer in wolf diets varies considerably by population, by pack, and among individuals, although much of the variation among populations is explained by differences in availability of deer and alternative large-bodied mammalian prey (Darimont et al. 2004). As a result, wolves in island

populations rely more heavily on deer than in mainland populations, where other large mammalian herbivores are available and deer are less abundant (Szepanski et al. 1999, Darimont et al. 2004). Therefore, on islands like POW, wolves are linked strongly to deer, although salmon subsidize wolf diets during parts of the year, thereby reducing dependency on deer to some extent (Szepanski et al. 1999).

The primary drivers of deer population dynamics in southeastern Alaska include winter severity, habitat quality, and predation by wild carnivores and humans. Winter severity is highly variable through time and space in southeastern Alaska and coastal British Columbia (Shanley et al. 2015), and plays a key role in governing deer survival and population dynamics (Person et al. 2009, Gilbert 2015). Deep snow increases the cost of movement by deer (Parker et al. 1984) and buries forage (Parker et al. 1999, White et al. 2009), reducing landscape connectivity, carrying capacity, and decreasing foraging efficiency (Kirchhoff 1994, Parker et al. 1999, Hanley et al. 2012). Consequently, deer populations can decline sharply in or following severe winters, particularly if they occur sequentially (Brinkman et al. 2011, Alaska Department of Fish and Game 2013). Whereas adult deer are relatively insensitive to winter severity except in extremely severe winters (Farmer et al. 2006, Person et al. 2009, Gilbert 2015), juvenile animals have fewer body reserves and shorter leg length than adults (Parker et al. 1984, 1993), resulting in reduced juvenile survival during even moderately severe winters (Farmer et al. 2006, Gilbert 2015). In addition, fecundity may be depressed in the spring following a severe winter due to malnutrition (Hanley 1984, Gilbert 2015). In the years following a severe winter or series of winters, it is thought that deer may potentially remain at low population levels if predation rates are high, but should otherwise recover (Alaska Department of Fish and Game 2013).

Habitat quality is another key driver of deer population dynamics in southeastern Alaska, and the effects of habitat quality interact with the effects of snow and predation. Industrial timber harvest has converted old-growth forest to even-aged forest stands throughout southeastern Alaska, but especially in the southern portions of the Alexander Archipelago including POW. During early successional stages before the forest canopy regenerates (< 30 years old), logged stands are highly productive for forage biomass, but lose understory forage plants as the canopy increasingly intercepts sunlight (Alaback 1982, Hanley et al. 2012). This is referred to as the stem-exclusion phase of post-logging forest succession, which may persist for >150 years. Winter snowfall modifies the value of these seral stages for deer, as snow readily accumulates in young second-growth stands, effectively rendering forage unavailable, while the thick canopy of old second-growth stands intercept snow well (Kirchhoff and Schoen 1987). Deer use of both young and old second-growth has been associated with increased mortality risk (Farmer et al. 2006, Person et al. 2009), suggesting that landscapes dominated by second-growth habitats are likely to negatively impact deer populations over time. Brinkman et al. (2011) demonstrated that deer population densities were lowest in watersheds dominated by old second-growth following 3 severe winters. Subsequently, as deer carrying capacity and densities decline in logged landscapes, wolf densities are likewise expected to decline (Person 2001).

Timber harvest also affects wolves and deer by increasing the density and distribution of roads. Roads provide hunters and trappers with access to otherwise remote areas (Brinkman et al. 2009), resulting in increased wolf (Person and Russell 2008) and deer mortality (Person 2001). If roads are closed (or “stored” for future use via temporary closure using barriers) in years following a timber sale, trappers and hunters with all-terrain vehicles and snow machines often continue use of them by bypassing gates or other barriers. Hunters and trappers also harvest

wolves along shorelines via boat, making distance by ocean to human settlements an additional risk factor for wolves (Person and Russell 2008).

Management of wolves and deer on POW requires quality data at regular intervals (e.g., annually). However, populations of wolves and deer on POW are extremely challenging to monitor due to the difficulty and expense of surveying mammals in the high-relief, densely-forested landscape. The resulting paucity of empirical data on wolf and deer populations hinders the ability to make management decisions. Another approach to understanding population dynamics is to create a population model that can simulate how populations change through time and relative to influential variables (Person and Bowyer 1997).

Here, we develop and present a population model of wolves on POW with an overall goal of better understanding population dynamics and examining the relative influence of potential stressors on future wolf abundance. Many stressors affecting Alexander Archipelago wolves interact with one another and are expected to change over time, however, we were able to assess future population trends in a unified analysis by building on a model previously developed by Person and Bowyer (1997) and refined in 2001 (Person 2001). Specifically, we considered how changes to timber harvest and subsequent effects on forest succession and deer abundance, road building and closures, and hunting and trapping regulations affect wolf population dynamics. Our modeling philosophy was to not use a model that was overly simplistic and therefore biased nor a model that was too complex and therefore more uncertain than necessary (Burnham and Anderson 2002). Following this modeling philosophy, we only updated parameters in the existing model when new data were available (Table 1). We used this population model to evaluate 6 possible future scenarios that were developed by a group of experts and to conduct sensitivity analyses to measure relative strength of influence of single parameters on changes in

wolf and deer abundance. The objective of the modeling effort was to estimate relative changes in wolf abundance under different scenarios (or environmental conditions) through time in the POW study area (i.e., Game Management Unit 2).

METHODS

Study Area

This population assessment focuses on the wolf population occupying POW and closely adjacent islands (henceforth jointly referred to as the POW study area; Figure 2), also referred to by ADF&G as Game Management Unit 2 for wildlife management purposes. We focus on the POW study area because it historically has supported a large portion of the population of Alexander Archipelago wolves in southeastern Alaska (Person et al. 1996), the population is partially isolated (Weckworth et al. 2005, Breed 2007, Cronin et al. 2015b), and it has the greatest concentration of stressors to wolves, including intensive timber harvest and road density.

The POW study area is typical of the coastal temperate rainforest ecosystem of southeastern Alaska and coastal British Columbia in many ways, except the POW study area has milder winter conditions and gentler topography than the rest of the region. The abundant year-round precipitation (>300 cm per year) falls as rain during summer, and as a mixture of rain and snow during winter due to the moderate variation in annual temperatures (Shanley et al. 2015). The climate in the region is projected to become warmer and wetter, but with more of the annual total of precipitation falling during winter (Cherry et al. 2010, Shanley et al. 2015). Although different global emissions and climate scenarios produce divergent predictions of future winter snowfall, most predict decreases in total winter snowfall (Littell 2015, Shanley et al. 2015). However, increased storm severity has been documented already, and is anticipated to increase

yet further in the future, and as a result, the frequency of extreme snowfall events is unknown (Haufler et al. 2010).

The abundant year-round precipitation in the region helps produce a diversity of habitat types including old-growth forest types, numerous lakes, rivers and estuaries, alpine and subalpine vegetation above ~400 m, and muskeg heaths (Farmer and Kirchhoff 2007, Alaback and Saunders 2013). In addition, industrial timber harvest has transformed the region, with disproportionate amounts of commercially valuable old-growth forest removed from the POW study area relative to the region as a whole (Albert and Schoen 2013). Albert and Schoen (2007) estimate that 40% of the productive forest land on North POW Island has been logged, along with 9% of this forest type on South POW Island (a less productive and accessible portion of the island), for a total of approximately 145,000 hectares (359,000 acres) within GMU 2 as of 2004.

In addition to acting as primary prey of wolves, deer are important prey for both humans and bears. Much of the deer harvest in southeastern Alaska is concentrated on POW due to the ease of access on the widespread road system, high deer densities, and liberal harvest regulations (Brinkman et al. 2009). Current regulations allow for the harvest of 4 male deer per Alaska resident, and 1 additional female deer per qualified state subsistence user. In addition to human predation, deer fawns also are preyed on occasionally by eagles and much more frequently by black bears (*Ursus americanus*; Gilbert 2015). Black bears exist at high densities on POW, and can prey heavily on deer, consuming nearly half of fawns born annually (Gilbert 2015), and occasionally depredating adults (Person et al. 2009, Gilbert 2015).

Model construction and parameterization

We present a wolf population abundance model for the POW study area, which is based on a previous model developed by Person and Bowyer (1997) and revised by Person (2001). Here, we describe the fundamental structure of the model, and highlight differences between the model we present and the previous Person (2001) model (henceforth the “2001 model”). The 2001 model used data specific to wolves in the POW study area when available, as well as data and relationships from studies of wolves and deer in other ecosystems when data specific to the POW study area were not available. The base 2001 model exhibited good performance for describing population dynamics when validated on other systems with more complete data such as deer at the George Reserve, wolves on Coronation Island, and wolves and moose at Isle Royale (Person et al. 2001). Therefore, in general, we updated the 2001 model only when new data from southeastern Alaska were available, retaining relationships and parameter estimates from the 2001 model if not.

With our updated model, we simulated the effects of predicted environmental changes on wolf abundance. The basic structure of the model includes the major factors expected to influence future wolf abundance: changes to deer carrying capacity, projections of winter severity, and harvest rates by humans. Secondary drivers are considerably more complex (Figure 1), resulting in relationships that are either one-way, or involve density-dependent feedback loops (Figure 3).

We describe in detail the updates we made to the structure and parameters of the wolf population model in Supplementary Information 1, and list new data sources in Table 1. Below, we describe the basic model structures. We modeled wolf population dynamics in the POW study area as a cumulative sum of dynamics of 31 hypothetical, spatially-explicit, contiguous

wolf “packs” (Figure 2), with each wolf home-range represented by a polygon with a mean size of 303 km² (SD = 87). We use the term “packs” to describe wolves in each polygon; however, wolves in a polygon don’t have to be organized into a single pack, although the dynamics of all packs in a given polygon are linked. Empirical estimates of wolf home-range sizes are variable, ranging from 260 km² (SE = 48; Person 2001) to 535 km² (Alaska Department of Fish and Game 2015b). We used the same pack polygon boundaries established by Person (2001) and assumed a closed population of wolves in the POW study area, although we allowed wolves to disperse among all pack polygons without geographic restrictions, which partially allowed packs to be more realistically dynamic in terms of recovery from local extinction. We recognize that pack areas are dynamic, however, we did not have adequate data to include this additional level of complexity in the model and Person (2001) previously addressed the potential effects of this assumption, which were relatively minor (see Discussion).

Within each wolf pack i , annual wolf numbers are described using the formula:

$$P_{t+1(i)} = P_{t(i)} + R_{pt(i)} - T_{t(i)} - D_{t(i)} - M_{t(i)} + I_{t(i)}$$

where $P_{t(i)}$ is the size of the wolf pack prior to parturition in pack area i , $R_{pt(i)}$ is recruitment, $T_{t(i)}$ is wolves harvested, $D_{t(i)}$ is dispersal, $M_{t(i)}$ is natural mortality, and $I_{t(i)}$ is immigration from other packs. Recruitment, natural mortality, and dispersal probability were modeled as density dependent, based on the ratio of deer available: deer consumed for each wolf pack (Supplementary Information 1, Equations 7, 9 and 10), while natural mortality and dispersal are compensatory with mortality from human harvest (i.e. human harvest reduces rates of natural mortality and dispersal; Person and Bowyer 1997). Human harvest of wolves was determined for each pack based on road density and distance via ocean from the nearest human settlement

(Supplementary Information 1, Equation 8). Individual wolf packs affect overall wolf pack dynamics by contributing dispersing wolves in a density-dependent manner that could colonize vacant packs. We modified the model so that if dispersing wolves did not colonize a vacant pack area in year t , dispersers survived from year to year in a shared, population-wide pool, thus increasing the disperser pool and further increasing pack dynamics.

The deer sub-model was an important component of the wolf population model, and we describe the key aspects of this model below (details in Supplementary Information 1). The deer population at time t was calculated as:

$$U_{t+1(i)} = U_{t(i)} + R_{ut(i)} - BA_{t(i)} - CP_{at(i)} - H_{t(i)}$$

where $R_{ut(i)}$ is recruitment into the deer population in pack area i , $BA_{t(i)}$ is predation mortality of adult deer by black bears, $CP_{at(i)}$ is predation mortality of deer by wolves, and $H_{t(i)}$ is death from human hunting. C , the per-capita wolf predation rate (15 deer/wolf/year) was based on a wolf diet estimate from a stable isotope analysis (Szepanski et al. 1999), and thus represents a minimum value, given that wolves do not necessarily consume all of a deer carcass. $P_{at(i)}$ is the average of spring and fall population sizes of wolves in year t . Similar to the wolf model, the deer model was density-dependent. Recruitment scaled with proximity of the deer population in pack area i to the carrying capacity of deer in the pack area (Supplementary Information 1, Equation 2). We modeled predation of fawns by black bears as density-dependent as well, with the proportion of mortality that was compensatory increasing as the deer population approached carrying capacity, K (Supplementary Information 1, Equation 3). Deer carrying capacity in each pack area was derived from the deer habitat capability index, (deer HCI; Suring et al. 1993),

which estimates the maximum number of deer that can be supported during winter in a specified area (United States Forest Service 2008). Adult deer mortality due to hunting, predation by black bears and wolves were treated as completely additive. Hunting mortality was a product of road length, based on a regression relationship (Supplementary Information 1, Equation 5) established by Person and Bowyer (1997).

Scenario development

We developed scenarios for analysis using the model that spanned the range of possible future conditions in the POW study area, rather than analyzing all combinations of future conditions. The conditions for each scenario were based on proposed or planned land use and resource management actions, as well as on modeled future climate scenarios for the region, downscaled from global climate models (calculation of winter severity frequency from climate scenarios is described in Supplementary Information 1). We developed 6 scenarios during a technical model review workshop with participants from key management agencies and technical experts in population modeling, spatial analysis, and wolf ecology, Anchorage, Alaska, March 18–19, 2015.

Scenarios varied across likely future changes to timber harvest, road building and/or closures (i.e. decommissioning), effects of climate change on frequency of severe winters, and wolf harvest regulations. We considered changes to vegetation due to timber harvest, including:

- 1) no future timber harvest after 2014 (i.e., forest successional change from past logging only);
- 2) a transition to harvest of second-growth forest on Tongass National Forest lands (i.e. the young growth transition currently in planning by the U.S. Forest Service);
- 3) continued harvest

of old-growth at the rates observed from 2008–2014; 4) increased harvest of old-growth forest at the rates observed from 1995–2000; and 5) maximum harvest of old-growth forest allowable under the 2008 Tongass Land Management Plan. We also varied the rate of future logging assumed to occur on State of Alaska, Alaska Mental Health Land Trust and Alaska Native Corporation lands among these alternatives. Details and assumptions associated with these possible future vegetation conditions are included in Supplementary Information 2.

We considered 5 alternative conditions for roads: 1) no change in road length from 2014 levels; 2) road decommissioning at levels planned in the POW Travel Access Management Plan (i.e., -2.2 % total road length, implemented during 2015-2025, United States Forest Service 2009); 3) road decommissioning at increased levels in the POW Travel Access Management Plan (i.e., -28.7% total road length, implemented during 2015–2025); 4) road decommissioning at maximum levels in the POW Travel Access Management Plan (i.e. -32% total road length, implemented during 2015–2025); and 5) road construction necessary to access new old-growth harvest areas if the maximum old-growth harvest scenario takes place. Road construction necessary to access new old-growth was calculated based on a regression relationship between existing total road length and acres of timber harvest in the wolf pack areas, the approach recommended by the Tongass Land Management Plan for estimating the effect of new timber harvest on road length (United States Forest Service 2008). We used the resulting slope (i.e. regression coefficient, $\beta = 0.0385$, $SE = 0.0026$, $R^2 = 0.88$), which specifies 0.0385 km of road construction per hectare of new logging.

Wolf harvest regulations that we considered ranged from complete closure of regulated harvest (0% reported harvest), to closure of harvest within a harvest season if reported harvest exceeded a fixed percentage (20% and 30%) of the previous fall population (i.e. a harvest “cap”).

In addition, Person and Russell (2008) found that 13 of 31 wolves harvested by humans were not reported. As a result, we use regression relationships to predict reported harvest based on road density and distance to nearest town via ocean (see Supplementary Information 1, equation 8), multiplied the result by an unreported harvest scalar of 1.72, equivalent to total harvest ($n = 31$) divided by reported harvest ($n = 18$), then applied a harvest cap to the reported portion of the predicted harvest for each pack if the cap threshold was exceeded at the population level.

Combining these factors, along with possible future frequencies of severe winters (Supplementary Information 1), we created 6 scenarios with input from workshop participants for evaluation (Table 2). Across scenarios, we hypothesized that Scenario A would be most favorable for wolf abundance, Scenario B would be the most favorable and reasonably likely scenario under current agency policy, and Scenario E would be least favorable for wolf abundance. We also included a No Change scenario, which represented ongoing changes in forest succession and habitat values from past logging, with minimum additional change or management action in the future (i.e. no future timber harvest, average frequency of severe winters, 20% cap harvest cap, and no change to road length).

In subsequent peer review, one reviewer argued that scenario D was much more probable than scenario B. We don't have any additional data to help predict which future scenario is most likely and therefore we continue to treat scenario B as the base. In addition, it should be noted that the absolute values (e.g., wolf abundance) for any scenario should be treated with caution since the values (e.g., deer K based on HCI) used to calculate wolf K for any pack are hypothetical. Inference should be based mostly on relative comparison of scenarios, which is much less affected by model conditions, than absolute values. Therefore, outputs from the model under the 6 scenarios are presented as percentage change from 2015 to year t , ending in

2045, rather than as abundance. We restrict our output to relative measures to avoid misinterpretation of abundance estimate outputs as predictions of future total population size.

We chose a 30-year timeframe, from 2015 to 2045, for model simulations because it encompassed enough years for the population dynamics of long-lived animals such as deer and wolves to stabilize and respond to environmental change, but was short enough to minimize uncertainty in future management, climate, socioeconomic, and other sources. In addition, the 20-year initiation period, from 1995–2015, allowed for the burn-in of the model to historical wolf harvest, timber harvest, and road data, as well as to the arbitrary starting conditions of the deer and wolf population sizes. “Burn-in” describes the period in a model when the initial conditions chosen partially dictate model results, before the underlying model structure has had enough annual cycles to remove these effects.

Sensitivity analysis

To isolate the effect of changes to vegetation, road length, frequency of severe winters, and wolf harvest regulations in the scenarios, we perturbed each of these variables separately across the range of values found in Scenarios A–E, while holding all other variables at Scenario B values. We also tested model sensitivity to wolf diet composition and deer harvest regulations, examining wolf diets comprised of 9.5 deer/wolf/year (i.e. 28% deer in the diet), 20.5 deer/wolf/year (i.e., 60% deer in the diet), 26 deer/wolf/year (i.e. 77% deer in the diet; Person 1996), in addition to the 15 deer/wolf/year used in scenarios (i.e., 44.7% deer in the diet). As with scenario results, we present results of sensitivity analysis as percent change in abundance over 30 years from 2014 levels (i.e., total change by 2045) and base interpretation mostly on relative comparisons.

RESULTS

Scenario development

At model initiation in 1995, the study area contained approximately 424,656 ha of productive old growth forest, 134,621 ha of logged forests and 410,720 ha of other land cover types (Table 3). Of the forests that had been logged, 73% were ≤ 25 years old and 27% were > 25 years old and estimated to be in stem-exclusion (i.e., low deer K) for the purpose of the deer habitat model. By 2015, the total logging had increased to 165,664 ha, with a reversal in the dominant age class toward older (> 25 yr) second growth (69%) and lower proportion of early successional forests (31%) (Table 3). Under the ‘No change’ scenario with no additional logging after 2014, we expect 100% of these stands to be in closed-canopy stem exclusion by 2045. By 2045, Scenario B projected a total of 188,116 ha (86% in stem exclusion), Scenario C projected a total of 195,733 ha. (89% in stem exclusion), Scenario D projected a total of 207,961 ha. (90% in stem exclusion), and Scenario E projected a total of 216,065 ha. (93% in stem exclusion) as having been logged (Table 3). These changes represent a decline of approximately 13% in carrying capacity for deer from 1995 to 2015 (Figure 4). Subsequently, under the ‘No change’ scenario (and Scenario A), we estimated an additional decline of 6% before the trajectory bottoms out in 2035. Larger declines in carrying capacity were projected to occur under Scenario B (-9%), Scenario C (-11%), Scenario D (-14%) and Scenario E (-17%) through 2045 (Figure 4).

Scenario outcomes

Declines were observed across all scenarios in both wolf abundance (range: -5% to -20%) and deer abundance (range: -21% to -33%) (Table 4, Figure 5). Scenario outputs for deer and wolves differed over time (Table 4, Figures 4 and 6) and relative to one another. The smallest decline in

wolf abundance (-5%, 95% CI = -16, 1) resulted from Scenario A (Table 2, Figure 6), which included no further timber harvest (i.e., natural succession only from 2015 onwards), planned decommission of roads, a low future frequency of severe winters, and no reported wolf harvest (although unreported wolf harvest was included). However, Scenario A also resulted in the largest decrease in deer population among the scenarios, (-33%, 95% CI = -48, -22). This decrease occurred despite less frequent severe winters because wolf numbers were high due to no reported harvest while deer carrying capacity continued to diminish due to natural succession and continued hunting pressure in accessible watersheds. The smallest decline in deer numbers (-21%, 95% CI = -39, -7) resulted from the No Change Scenario, which was equivalent to Scenario A for vegetation, but included no road decommissioning, average winter severity, and a 20% cap on reported wolf harvest. The largest declines in wolf abundance (-20%, 95% CI = -29, -15) and second largest decline in deer abundance (-32%, 95% CI = -51, -18) was produced by Scenario E, which involved maximum harvest of old growth as targeted in the Tongass Land Management Plan, with accompanying road construction associated with timber harvest, a high frequency of severe winters, and a 30% cap on reported wolf harvest.

Scenario B resulted in an 8% decline in wolf abundance (95% CI = -12, -6) and a 21% decline in deer abundance (95% CI = -38, -9). Scenario B involved the implementation of current and near-future timber sales (see Supplementary Information 2 for details), a transition to harvest of primarily young-growth forest, the planned decommission of roads, average frequency of severe winters, and a 20% cap on reported wolf harvest. Other scenarios all showed intermediate levels of decline in deer and wolf abundance (Table 4).

Sensitivity results

Wolf and deer abundance declined across most of the sensitivity models because of ongoing changes in post-logging forest succession, declines that were also observed under the base model, Scenario B. The results here do not allow for the comparison of absolute influence of variables on the model (e.g., is a 10% change in deer carrying capacity, or a 10% change in road length more influential on wolf abundance?) because each variable is measured on a different scale. Instead, these sensitivity analyses allow us to evaluate how the different levels of each variable that are combined to make up the future scenarios affect wolf and deer abundance (e.g., is the decrease in carrying capacity due to continued old-growth timber harvest, or the decrease in road density due to planned decommissioning more influential on wolf abundance?).

The most influential variable on wolf abundance in the model was wolf diet composition (Table 5, Figure 7), with changes in wolf abundance from 2015 levels ranging from an increase of 35% (95% CI = 29, 45) if wolf diet was specified as 9.5 deer/wolf/year, to a decrease of -54% (95% CI = -74, -43) if wolf diet was specified as 26 deer/wolf/year. Deer abundance changes also varied widely depending on wolf diet composition, with a value of 9.5 deer/wolf/year resulting in an -8% (95% CI = -19, -1) decrease, while a value of 26 deer/wolf/year resulted in a decline of -49% (95% CI = -76, -30), the largest relative decline of deer recorded among the sensitivity analyses. Predictably, intermediate values for wolf diet composition, 15 deer/wolf/year and 20.5 deer/wolf/year, had intermediate effects (Table 5, Figures 7d and 9c). Given the sensitivity of the model to diet composition and the large differences in rates of wolf and deer declines between 15 deer/wolf/year (isotope analysis) and 20.5 deer/wolf/year (scat analysis and other supporting data), the rates of change described under scenario B conditions (with 15 deer/wolf/year) are likely conservative.

The second most influential variable was road length (Table 5, Figure 7b & 9b). Perturbing road length resulted in changes in wolf abundance (relative to 2014 levels) ranging from an increase of 8% (95% CI = -1, 13) if the maximum potential amount of decommissioning in the POW Travel Access Management Plan is implemented (i.e., 2,281 km decommissioned, 38% decrease in road density), to a decrease of -20% (95% CI = -25, -18) if roads are built in order to implement the maximum level of timber harvest described in the Tongass Land Management Plan are built (i.e. 1,876 km constructed, 23% increase in road density). This maximum road decommissioned level resulted in a decline of deer by -20% (95% CI = -39, -7), while road construction reduced deer abundance in the model by -30% (95% CI = -47, -19), a relatively narrow range of declines in comparison with wolves (Table 5, Figures 7 and 9). Although we could not justify restricting boat access in sensitivity analysis given the difficulty of implementing such a restriction, we expect that changes in this parameter would have produced similar results to road restrictions since both forms of access affected wolf harvest.

Aside from the long-term trajectory of declining habitat for deer as forests transition into stem-excluded conditions, vegetation-driven change to deer carrying capacity among scenarios was less influential than road length/density or wolf diet at the levels considered in this analysis (Table 5, Figures 7a and 9a). Effects ranged from a decrease in wolf abundance from 2015 levels of -4% (95% CI = -8, -2) if carrying capacity was maintained at 2014 levels (i.e., 73,419 deer) to decreases of -9% (95% CI = -15, -5), -10% (95% CI = -16, -6), and -9% (95% CI = -15, -6) given continued, increased, and maximum levels of harvest of old-growth forest (i.e., K reduced by 8,166 deer, 10,553 deer, or 12,802 deer from 2014 levels, respectively). As with previous variables, deer declines were greater than wolf declines, ranging from -16% (95% CI = -36, -2) for stable carrying capacity, to -22% (95% CI = -42, -9), -25% (95% CI = -42, -12), and -26%

(95% CI = -43, -14) for continued, increased, and maximum levels of harvest of old-growth forest. No future timber harvest, or a transition to harvest of second-growth forest, resulted in intermediate declines in modeled wolf and deer abundance (Table 5, Figures 7 and 9).

Wolf harvest regulations that we considered had a very limited effect on wolf abundance mostly because of the manner in which we modeled the effects (see Discussion). Total closure of wolf harvest in the model resulted in declines in wolf abundance of -7% (95% CI = -21, 0), while wolf abundance declined by -8% (95% CI = -12, -6) and -8% (95% CI = -14, -4) for the caps on reported harvest of 20% and 30% of the previous fall's wolf population, respectively. For deer, total closure of wolf harvested resulted in a -35% change in abundance (95% CI = -54, -22), while the 20% and 30% harvest caps resulted in equivalent declines of -21% (95% CI = -38, -9), -21% (95% CI = -39, -9) because average wolf harvest under these caps was similar.

Given the strength of the influence of roads on wolves, we explored the effects of harvest regulation under maximum road decommissioning conditions (i.e., an average 38% decline in road density per pack), and found that future wolf abundance increased from 2014 levels under all three harvest regulations (Figure 8). A small increase in abundance (5%, 95% CI = -8%, 13%) and the largest decrease in deer (-27%, 95% CI = -47, -14) were produced under the 0% reported harvest regulation. Increases in wolf abundance were similar under the 20% cap on harvest (9%, 95% CI = 3%, 12%) and the 30% cap on harvest (9%, 95% CI = -1%, 14%), as were declines in deer abundance (-19% and -20% respectively). Compared with the harvest regulation results under planned decommissioning (i.e., sensitivity analysis), differences in wolf abundance (12% difference) were smallest and differences in deer abundance were largest (8%) for 0% harvest, while differences were smaller in wolf (17%) and deer abundance (<2%) for the 20% and 30% cap on reported harvest.

Frequency of severe winters (Table 5, Figures 8 & 9) also was not highly influential for deer and wolf abundance, with low frequencies of severe winters (i.e., 7 severe winters per 100 years) causing declines of -6% (95% CI = -10, -4) in wolf abundance, and -20% (95% CI = -35, -9) in deer abundance. Average frequencies of severe winters (i.e., 8 severe winters per 100 years) caused declines of -8% (95% CI = -12, -6) in wolf abundance and -21% (95% CI = -38, -9) in deer abundance, whereas high frequencies of severe winters (i.e., 10 severe winters per 100 years) caused declines of -13% (95% CI = -26, -5) in wolf abundance and -25% (95% CI = -47, -9) in deer abundance.

Finally, we explored the effects of changing deer harvest in the study area, by considering the most extreme possibility, no deer harvest (Figure 8d). We only considered this extreme condition because the model could not realistically quantify the effects of different levels of deer harvest in its current form. No deer harvest had a large positive effect on both wolf and deer abundance compared to 2015 levels, increasing wolf abundance by 22% (95% CI = 31, 17), and deer abundance by 30% (95% CI = 20, 37). Although an extreme and unrealistic perturbation of the deer harvest variables, it indicated that changes to deer harvest regulations could provide a tool for increasing wolf and deer abundance and this action warrants further investigation that account for buck and doe harvest, which is not possible in the current model structure.

DISCUSSION

Model results of wolf abundance under all 6 scenarios indicated that, following an initial increase during the first 5 years, abundance will decline through 2045 with declines varying from 5% (Scenario A) to 20% (Scenario E). Wolf population persisted for every scenario, however, we did not attempt to define an extinction threshold. Deer abundance also declined across all

scenarios, without an initial increase, and declines were larger and less variable across scenarios than those of wolves (from 21% for Scenario A to 32% for Scenario E). These rates of decline are almost certainly conservative because the scenarios were modeled with a conservation estimate of wolf consumption rate of deer based on isotope work. Rates of declines would be >15% larger for deer and wolves if we used consumption rates >20.5 deer/wolf/year (see Table 5 and discussion of assumptions).

Interpreting the differences among scenario outcomes requires an understanding of the influence of each parameter on the model. Based on our sensitivity analysis, the most important influences on future wolf abundance were road density and deer harvest, although timber harvest (i.e., vegetation change), frequency of severe winter, and wolf harvest regulation also affected wolf abundance to a lesser degree. Overall, roads had a strong effect on wolf abundance, both through reductions in deer hunting and through local reductions in wolf harvest in high-road-density watersheds. Person and Russell (2008) found that where road densities were above 0.9 km/km², wolf harvest was unsustainable. Currently, 31% of the hypothetical packs have road densities ≥ 0.9 km/km² and the planned road decommissioning across POW would not reduce this percentage. However, increased road decommissioning yielded 13% of packs above this threshold in 2045, whereas maximum decommissioning yielded 0% of packs above this threshold, and road construction associated with maximum harvest of old-growth forest resulted in 52% of packs over this threshold. Packs above the road density threshold were often extirpated, although re-colonized by the shared pool of dispersers, effectively acting as local population sinks. The strength of the population response to a greater proportion of “sink” packs suggests that these road-induced sinks are important not only for local wolf dynamics, but for population dynamics at the GMU level as well. The effect of road changes to deer harvest rates

must also be considered (Figure 9b). In addition to roads, boat access affects both wolf and deer harvest. Although we modeled the relationship between wolf harvest and boat access, we did not consider the sensitivity to this form of access because we had no basis for varying access in existing management plans. However, management should consider how all forms of access might affect wolf populations (Person and Logan 2012).

Aside from the long-term trajectory of ongoing forests succession across all scenarios, additional changes in vegetation among scenarios had relatively small effect on wolf abundance (-7% to -10% declines in abundance after 30 years). Indeed, the primary driver of change in estimated carrying capacity for deer during early phase of this study (1995 – 2015) was the relatively rapid rate of logging on Prince of Wales Island during the 1970's and 1980's. This study documents a significant shift in dominance from early-successional stands (<25 years old) in 1995 (73%) to late-successional stands in 2015 (69%). The rate at which post-logged stands entered stem-exclusion was approximately 4,000 acres per year, for a total increase of 215% between 1995 and 2015. As a result, carrying capacity for deer in 2015 was estimated at 88% of what it was in 1995 (a loss of 10,282 deer equivalents, or 1,142 deer equivalents/year), and 73% of what it was in 1954 (a loss of 26,921 deer equivalents, or 441 deer equivalents/year). This change, the time-lagged effect of past logging on current and future habitat conditions for deer, has been described as the 'succession debt' in the system by Person and Brinkman (2013), and constitutes a significant proportion of forest change anticipated under any of the future management scenarios (Table 3). Looking forward, with no additional logging assumed after 2014 (Scenario A & 'No Change'), stem-excluded second growth was projected to increase 355% (165,664 ha,) from 1995 conditions. This trajectory can be expected to bottom out by approximately 2035 (Figure 4). Carrying capacity would decline an additional 17% from 2015

under Scenario E, maximum old-growth harvest (a loss of 12,802 deer equivalents, or 426 deer equivalents/year), and reducing total carrying capacity to 60% of 1954 levels (Figure 4). In addition, we observed that deer abundance declined more than wolf abundance (i.e., each 1% decline in K caused a 1.5% to 3.5% decline in deer abundance) across vegetation scenarios.

We examined the effect of stabilization of carrying capacity at 2014 levels, equivalent to extensive habitat restoration across the entire study area, which resulted in a smaller decrease of -4% in wolf abundance (95% CI = -8, -2). This decline with stable carrying capacity was therefore the result of other variable in the model, which were held at Scenario B levels throughout all sensitivity analyses. There was no appreciable change in wolf abundance across the range of old-growth harvest possibilities and only small variation in declining abundance of deer (-22%, -25%, and -26% declines in deer over 30 years, for continued, increased, and maximum harvest of old-growth, respectively). This suggests that the increased road construction and human access associated with maximum old-growth harvest, rather than timber harvest itself, is likely responsible for the additional decline seen in worst-case Scenario E.

Wolf harvest regulation had a small effect on overall changes in wolf abundance and we attribute this finding to several possible reasons. First, the harvest cap both in the model and reality is implemented at the GMU level and therefore does not prevent localized overharvest and pack depletion as long as the cap on total harvest for the entire population is not exceeded (Person and Logan 2012). Second, a level of unreported harvest 1.7 times that of reported harvest occurs both in the model and in reality. Third, there is a time lag between actual population size and harvest cap, which is how we modeled the cap, because the cap is based on the population estimate from the previous fall (i.e., the most rapid and frequent theoretical timeline for a population survey, although only 4 population estimates have been conducted in the past 20

years). Wolf harvest in our model was determined by road density and distance by ocean from towns (i.e., where hunters reside) for each pack, not at the population (or GMU) level. Consequently, we rarely reached the population-level harvest cap in any scenario, although in reality, the harvest cap is often attained. For example, during sensitivity analyses, caps on reported harvest of 0%, 20%, and 30% resulted in modeled population-wide harvest rates of 3.5%, 10.3%, and 10.5% of the fall population, respectively, including unreported harvest, but not harvest of dispersers, which was relatively low due to the small dispersing proportion of the population. However, because some pack areas have high road densities (31% of packs >0.9 km/km² of road), these packs sustained extremely high harvest rates, and were depleted quickly in the model, which prevented the model from reaching the targeted harvest cap. Again, we could only reasonably model effects of changing road access, but boat access could have similar effects. These high-mortality areas (i.e. population sinks) could drain the population via death of residents and dispersers attempting to recolonize, with the harvest cap constantly adjusted downwards as the population incrementally declines. We suggest that attention should be paid by managers to the potentially large population effects of local sinks, to updating harvest caps regularly from ongoing population estimates, and to unreported harvest in determining sustainable wolf harvest regulations in the future (e.g., a cap on reported harvest of 17% of the fall population, multiplied by the unreported harvest scalar, produces a total harvest rate of 30%). We admittedly took a simple approach to modeling unreported harvest because data are limited (Person and Russell 2008); however, this is a potentially important factor and more recent data indicates that unreported harvest is still occurring at a rate ($8/5 = 1.6$) similar to what we modeled (Alaska Department of Fish and Game, unpublished data). Indeed, high unreported harvest rates have been implicated in failed or limited recovery of carnivores in other systems

(Liberg et al. 2012, Persson et al. 2015), and this cryptic harvest needs to be recognized and managed.

The future frequency of severe winters had a moderate effect on outcomes of scenarios, although variation among frequencies was small (0.07– 0.10). We also applied effects of a severe winter uniformly across all pack areas, but recognize that local climate conditions probably impact deer in some areas (i.e., areas at higher elevation or with poor winter habitat) more than others. The predicted future decline in the frequency of severe winters due to climate change will likely benefit the deer population in southeastern Alaska, although to what extent winter severity will change in the future depends on present and future carbon emissions. The future scenarios we evaluated for wolves included a range of future climate predictions, with wolves and deer abundance in the best-case Scenario A boosted by a low frequency of severe winters, in Scenarios B, C, and No Change benefiting slightly from an average future frequency of severe winters (although less frequent than historically), and in Scenarios D and E experiencing a continuation of current winter severity. Importantly, sequential severe winters are likely given the importance of climate cycles, but uncommon in our simple treatment of climate in the model. Indeed, sequential severe winters and associated declines in deer abundance in the mid-2000's appear to have exacerbated the effects of high wolf harvest, contributing additively to the current low wolf levels (Figure 5). Adaptive management of deer and wolf harvest following severe winters could help ameliorate such cascading effects in the future.

As with all models, our wolf population model relies on several key assumptions and has some inherent limitations that may be reduced with more time and data. First, wolf packs in reality occupy dynamic, shifting territories, while we model wolf pack areas as static through space and time. Person and Bowyer (1997) evaluated the effect of choice of pack area size, and

found a response in the model. As a result, they developed the 31 static pack areas used in this analysis, which roughly correspond in size to a wolf pack's home range size. We partially increased the dynamics of pack occupancy by allowing the disperser pool to survive from year to year, an update to the original model, yet it is likely that pack boundaries would shift through time, with unknown effects on model outcomes.

Second, we assumed, after much debate, an average predation rate of 15 deer/wolf/year in our scenarios, but model outcomes were highly sensitive to wolf diet composition. We chose this value based on stable isotope analysis, considered less biased than scat analysis (which resulting in 26/deer/wolf/year used in the 2001 version of the model). However, as one reviewer noted, isotope analysis does not account for prey that is killed but not consumed, partial consumption of prey, or differential consumption of prey among pack members, all behaviors known to occur with wolves. Nevertheless, the calculations of deer consumed in the model were based on the edible weight, rather than total weight, of deer (Person et al. 1996), thus accounting for some partial consumption. We elected to use 15 deer/wolf/year in the base model because this is a known level in the diet based on empirical evidence. We believe this is a minimum value, but we do not have adequate data to know how many additional deer are consumed per wolf/year nor the age/sex composition of those deer. As a result, our estimates of rates of declines for wolf and deer are conservative and may be much greater (>15% further decline) if wolves kill >20 deer/year or if wolves kill more does than bucks because our model is very sensitive to wolf consumption rates. For example, wolves declined by -54% (95% CI = -74, -43) in Scenario B if 26 deer/year were required (77% deer in annual diet; Person et al. 1996). Furthermore, wolf diets likely vary through time with deer and alternative prey availability, and through space with the availability of alternative prey across the landscape (Darimont et al. 2004,

2008). However, it is unlikely that wolves will require fewer deer/year than 15 (i.e., 45% of the annual diet; Szepanski et al. 1999), because outside of late summer/early fall, salmon are not available to wolves, and alternative ungulate prey are not available in the study area.

Additionally, we assume the population in the POW study area is closed to immigration and emigration, but do not take into account any genetic consequences of small population sizes (e.g., inbreeding depression), although such effects are likely if wolf populations decline to low levels. Finally, we do not account for any potential effects of disease, which could be important, especially for small population sizes. Given the assumptions and constraints present in our model, results should be used as a tool to evaluate relative effects of future change on wolf abundance, rather than to forecast population size or viability

In addition, interpretation of the effects of deer harvest on wolf abundance should be qualitative rather than quantitative. While elimination of deer harvest and road closures resulted in sharp increases in both deer and wolf abundance, results should be interpreted cautiously, as most deer harvested are males, but our model uses a constant per-capita reproductive rate based on an assumption of a 1:1 sex ratio. Thus, the demographic effect of deer hunting due to changes in roads would likely not prove as large as indicated in reality. Nevertheless, there is a substantial female component to deer harvest in the study area due to a federal subsistence season and illegal harvest, and male deer can affect fertility rates, with younger, less experienced males breeding less successfully and reducing conception rates as a result (Mysterud et al. 2002). Changes to deer harvest regulations could provide a tool for management of wolf abundance in this system.

For our study area, 4 empirical estimates of wolf abundance exist between 1994 and 2014 and are somewhat consistent with our model results, especially when considered alongside the stressors included in our model. Earlier empirical estimates were made based on deer abundance

and wolf vital rates from radio-collared wolves, resulting in estimated fall wolf numbers of 336 wolves (95% CI = 140, 532) in 1994 (Alaska Department of Fish and Game 2014) to 326 wolves (95% CI = 179, 473) in 2003 (Alaska Department of Fish and Game 2014). More recently, fall population size was estimated based on genetic capture-mark-recapture efforts, which resulted in an estimate of 221 wolves (95% CI = 130–378) in fall 2013 (Alaska Department of Fish and Game 2014) and an estimate of 89 wolves (95% CI = 50–159) in fall 2014 (Alaska Department of Fish and Game 2015a). Overall, the fall wolf population of GMU 2 has declined by approximately 75% since 1994, equivalent to a 6.7% decline annually, and the spring wolf population on POW may be <50 animals after accounting for reported and unreported harvest, although unreported harvest is currently not accounted for by ADF&G in estimating population change or setting harvest guidelines. Our model-based estimates of historical wolf abundance yielded annual wolf levels between 2000 and 2015 that were on average 28% higher than in 2014 (95% CI = 1, 44). In the model, this decline to 2014 levels indicated that high wolf harvest was compounded by sharp declines in deer abundance due to 2 severe winters, an increase in road density, and a rapid decrease in deer carrying capacity as younger clearcuts aged. Also, we noted a sharp decline in wolf abundance of 34% (95% CI = 32, 40) from 2010 to 2014, reflecting a time-lagged decline after the severe winter of 2008 reduced deer numbers (Figure 5). Deer in the model did not fully rebound following the severe winters, likely due to a combination of wolf predation pressure, increasing hunting pressure with more roads, and steadily declining carrying capacity due to forest succession. While our model predicts a smaller decline than suggested by empirical estimates, it is likely that this historical portion of the model under-estimates true wolf harvest during the 2000–2014 period, as wolf harvest reporting dropped off precipitously after an emergency closure partway through the trapping season in 1999 (Person and Russell 2008,

Bethune 2009), and we scale unreported wolf harvest based on a 1.7 multiplier of reported wolf harvest, thus including any negative bias in reporting statistics during this period. Furthermore, our unreported harvest scalar may be biased low since we only considered 13 collared wolves that were shot out of season and excluded 3 collared wolves that were trapped but were unreported for unknown reasons (Person and Russell 2008).

While these results are useful for understanding wolf dynamics and future trends in the Prince of Wales study area, it is less useful for predicting likely changes for wolves in Southeastern Alaska as a whole. Demographic parameters are likely different in other portions of the region due to increased nutritional constraints, as deer abundance is lower in many areas (Alaska Department of Fish and Game 2013), and other ungulates occur in low densities in other areas (e.g., mountain goat; White et al. 2011). However, results of our sensitivity analysis are applicable throughout the region and can be useful for qualitatively evaluating risk to wolves in other parts of southeastern Alaska and perhaps coastal British Columbia. The stressors included in our model are concentrated most in our study area, so future trends in deer carrying capacity, for example, are unlikely to be the same across the region. Accordingly, road density in the study area is also much higher than in the region as a whole, resulting in wolf and deer harvest pressure that is not representative of the region. Finally, if wolf diets vary across space and time, management actions affecting deer abundance will affect wolves depending on wolf diet composition.

In conclusion, our model conservatively predicts that wolves in GMU 2 will decline by -5 to 20% over the next 30 years, with potential for much higher declines depending on wolf diet composition. These declines can be attributed to population sinks in high-access areas due to both reported and unreported human harvest of wolves, and declines in deer numbers due to

long-term declines in deer carrying capacity. We encourage managers to consider not just management of wolves, but holistic management of an important predator-prey system in an altered landscape (see also Person and Brinkman 2013).

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TABLES AND FIGURES

Table 1. Chronology of additional data and publications used to update the Alexander Archipelago wolf population model.

Data Type	Data Source
Wolf reproduction	Person and Russell 2009
Wolf survival	Person and Russell 2008
Effect of roads on wolf mortality	Person and Russell 2008
Black bear Predation on fawns	Gilbert 2015
Black bear predation on adult	Gilbert 2015, Person 2009
Climate effects on winter severity	Littell 2015
Wolf Diet	Szepanski et al. 1999

Table 2. Description of scenarios evaluated using the wolf population model.

Scenario	Parameter	Condition
No Change	Vegetation	No change
	Roads	No change
	Wolf harvest	20% harvest cap
	Frequency of severe winter	Predicted average
Scenario A	Vegetation	No change
	Roads	Planned decommission
	Wolf harvest	No legal harvest
	Frequency of severe winter	Predicted low
Scenario B	Vegetation	Young growth transition
	Roads	Planned decommission
	Wolf harvest	20% harvest cap
	Frequency of severe winter	Predicted average
Scenario C	Vegetation	Continued harvest of old growth
	Roads	No change
	Wolf harvest	20% harvest cap
	Frequency of severe winter	Predicted average
Scenario D	Vegetation	Increased harvest of old growth
	Roads	No change
	Wolf harvest	30% harvest cap
	Frequency of severe winter	Predicted high

Scenario E	Vegetation	Maximum harvest of old growth
	Roads	Road construction
	Wolf harvest	30% harvest cap
	Frequency of severe winter	Predicted high

Table 3. Generalized land cover and forest conditions under baseline and future management scenarios in Game Management Unit 2 of southeastern Alaska, 1995 - 2045.

General Land Cover	Baseline		Future Scenarios in 2045				
	1995 (hectares)	2015 (hectares)	No Change (hectares)	Scenario B (hectares)	Scenario C (hectares)	Scenario D (hectares)	Scenario E (hectares)
Old-growth forest	424,656	397,040	397,040	374,588	366,971	354,742	346,639
Logged forest (all)	134,621	165,664	165,664	188,116	195,733	207,961	216,065
Early succession (≤ 25 yr)	98,230	50,821	0	25,468	21,502	20,328	14,050
Late succession (> 25 yr)	36,391	114,842	165,664	162,647	174,231	187,633	202,015
Other	410,720	410,720	410,720	410,720	410,720	410,720	410,720
Total	973,423	973,423	973,423	973,423	973,423	973,423	973,423

Table 4. Modeled changes in abundance of wolves and deer under future scenarios. Abundance is shown as % change from 2014 levels over 30 years, with 95 % confidence intervals. Rank reflects the decrease in wolf populations, with a rank of 1 indicating smallest relative decrease.

Scenario	Rank	Mean % change wolf	Mean % change deer
No change	3	-8 (-14, -5)	-21 (-39, -7)
Scenario A	1	-5 (-16, 1)	-33 (-48, -22)
Scenario B	2	-8 (-12, -6)	-21 (-38, -9)
Scenario C	4	-9 (-15, -6)	-22 (-39, -10)
Scenario D	5	-14 (-24, -8)	-28 (-48, -14)
Scenario E	6	-20 (-29, -15)	-32 (-51, -18)

Table 5. Sensitivity of wolf and deer abundance to changes in forest vegetation, road length, frequency of severe winters, wolf harvest regulation, and wolf diet composition. Abundance is shown as % change from 2014 levels over 30 years, with 95 % confidence intervals. Rank reflects the decrease in wolf populations, with a rank of 1 indicating least decrease.

Parameter	Perturbation description	Rank	Mean % change wolf	Mean % change deer
Vegetation	Stable K (restoration)	4	-4 (-8, -2)	-16 (-36, -2)
	No timber harvest	7	-7 (-13, -4)	-21 (-39, -7)
	*Transition to second growth	9	-8 (-12, -6)	-21 (-38, -9)
	Continued old growth harvest	14	-9 (-15, -5)	-22 (-42, -9)
	Increased old growth harvest	17	-10 (-16, -6)	-25 (-42, -12)
	Maximum old growth harvest	16	-9 (-15, -6)	-26 (-43, -14)
Roads	Maximum decommission	2	8 (-1, 13)	-20 (-39, -7)
	Increased decommission	3	4 (-6, 10)	-21 (-40, -6)
	*Planned decommission	9	-8 (-12, -6)	-21 (-38, -9)
	No change	15	-10 (-16, -6)	-22 (-41, -9)
	Road construction	19	-20 (-25, -18)	-30 (-47, -19)
Winter severity	Low frequency	5	-6 (-10, -4)	-20 (-35, -9)
	*Average frequency	9	-8 (-12, -6)	-21 (-38, -9)
	High frequency	18	-13 (-26, -5)	-25 (-47, -9)
Wolf harvest	Total harvest closure	6	-7 (-21, 0)	-35 (-54, -22)
	*20% cap on reported harvest	9	-8 (-12, -6)	-21 (-38, -9)
	30% cap on reported harvest	8	-8 (-14, -4)	-21 (-39, -9)
Wolf diet	9.5 deer/year	1	35 (29, 45)	-8 (-19, -1)

*15 deer/year	9	-8 (-12, -6)	-21 (-38, -9)
20.5 deer/year	20	-35 (-49, -27)	-36 (-59, -19)
26 deer/year	21	-54 (-74, -43)	-49 (-76, -30)

* Equivalent to Scenario B

FIGURES

Figure 1. Connections of major environmental drivers to wolf abundance in the coastal temperate rainforest of southeastern Alaska.

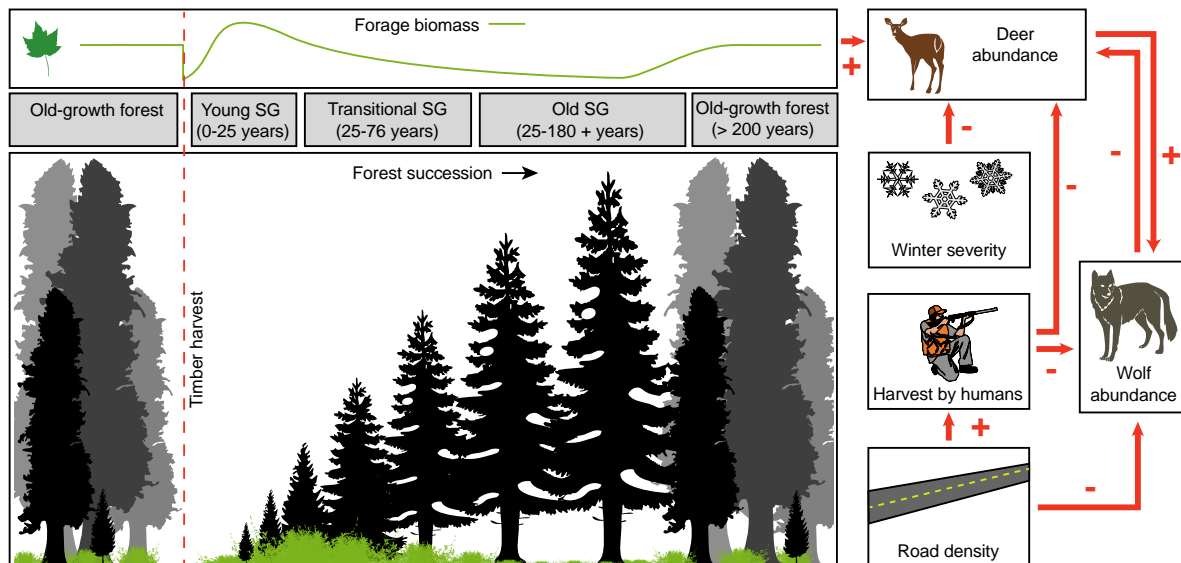


Figure 2. The study area, located on Prince of Wales and outlying islands in southeastern Alaska, with pack areas in the wolf population model outlined in blue and towns are shown as black circles. Shown is a) road density in km per km² in each pack area, and b) deer winter carrying capacity (K) based on the interagency deer habitat suitability index, which ranges from very high (76-130 deer per km²), to high (43-75 deer per km²), moderate (23-42 deer per km²), low (7.1-22 deer per km²), and very low (0-7 deer per km²).

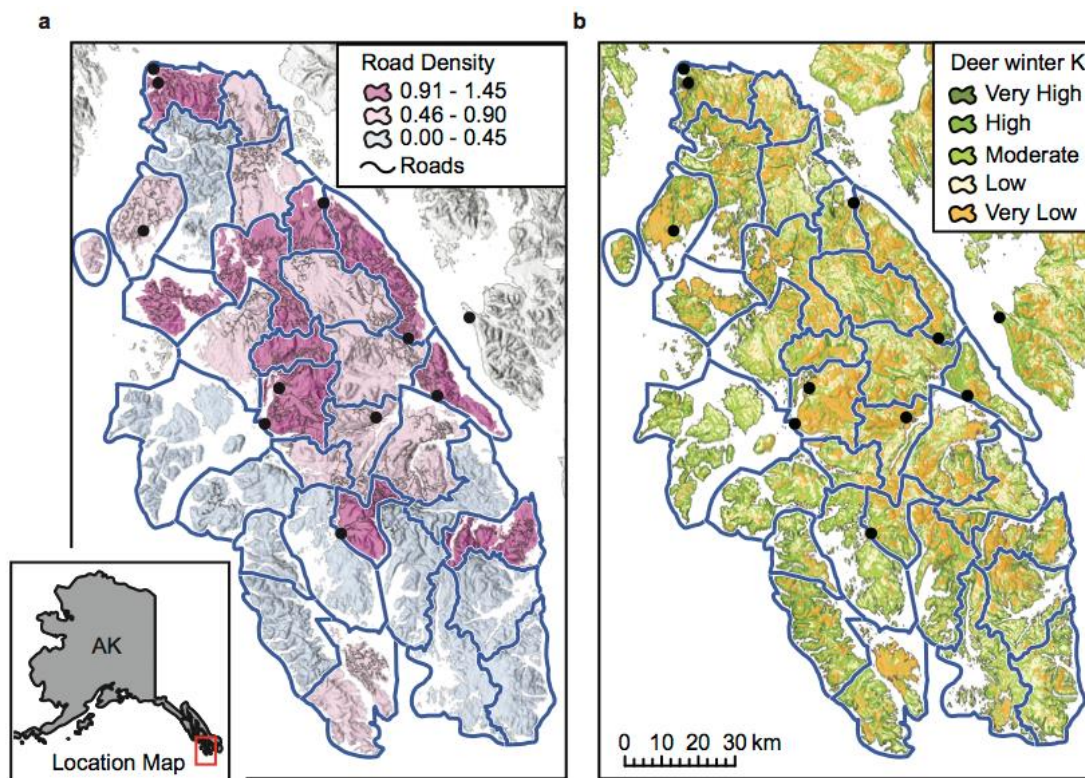


Figure 3. Relationship among primary model components, with equation numbers referencing Appendix A.

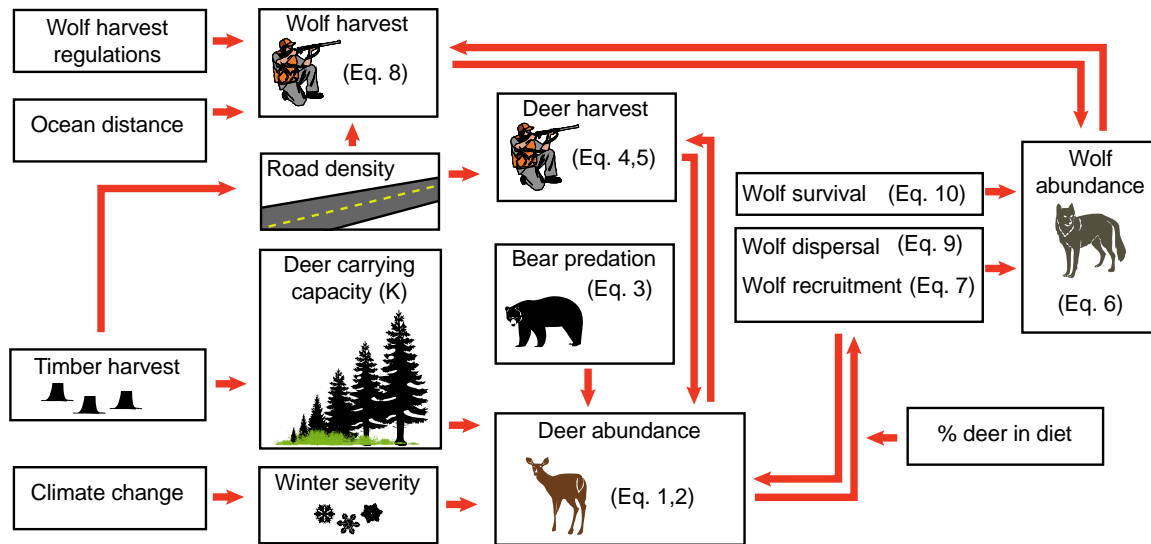
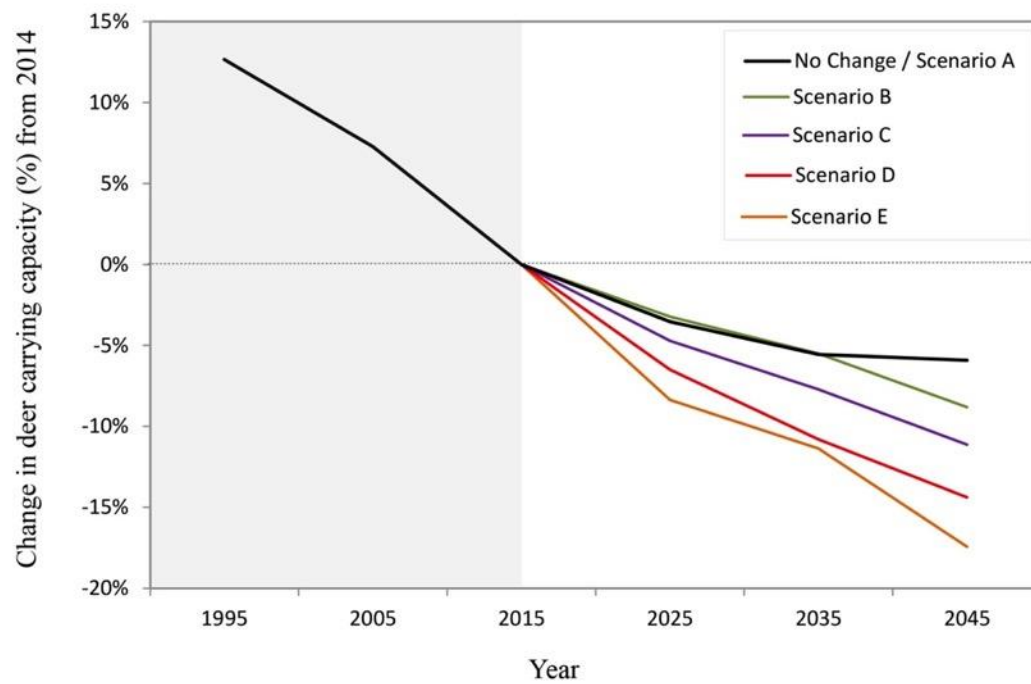


Figure 4. Estimated change in winter carrying capacity for deer under baseline conditions and future management scenarios in Game Management Unit 2 in southeastern Alaska, 1995 – 2045.



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Figure 5. Percent change in a) wolf abundance and b) deer abundance across model scenarios from 2014 levels, shown from the year 2000-2045. The grey box represents the years in the model (before 2015) where actual severe winters (dotted blue line) and reported wolf harvest were used as model inputs, while the white portion represents mean model predictions.

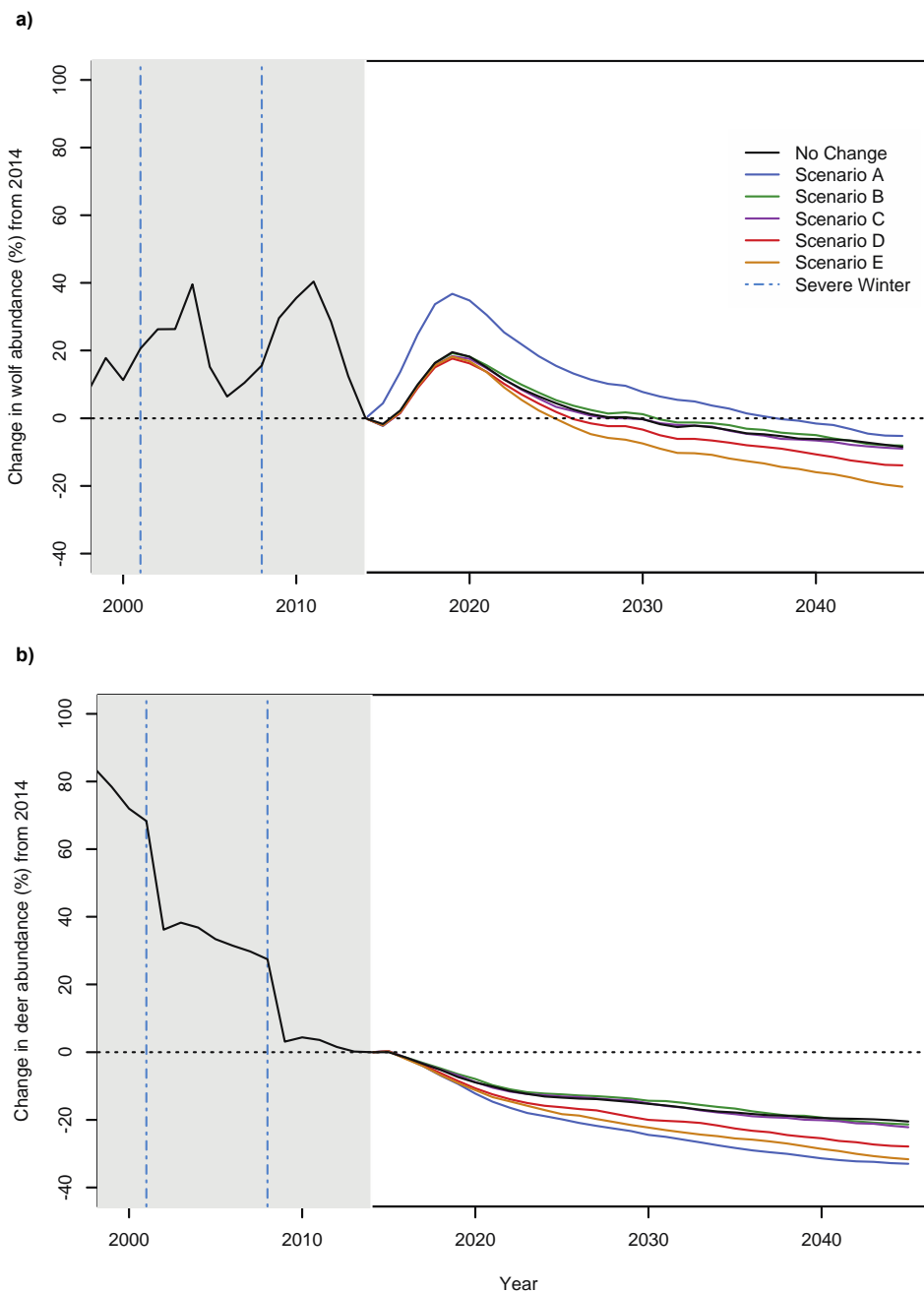


Figure 6. Percent change from 2014-2045 in wolf (grey) and deer (brown) abundance across model scenarios, with 95 % confidence interval bars.

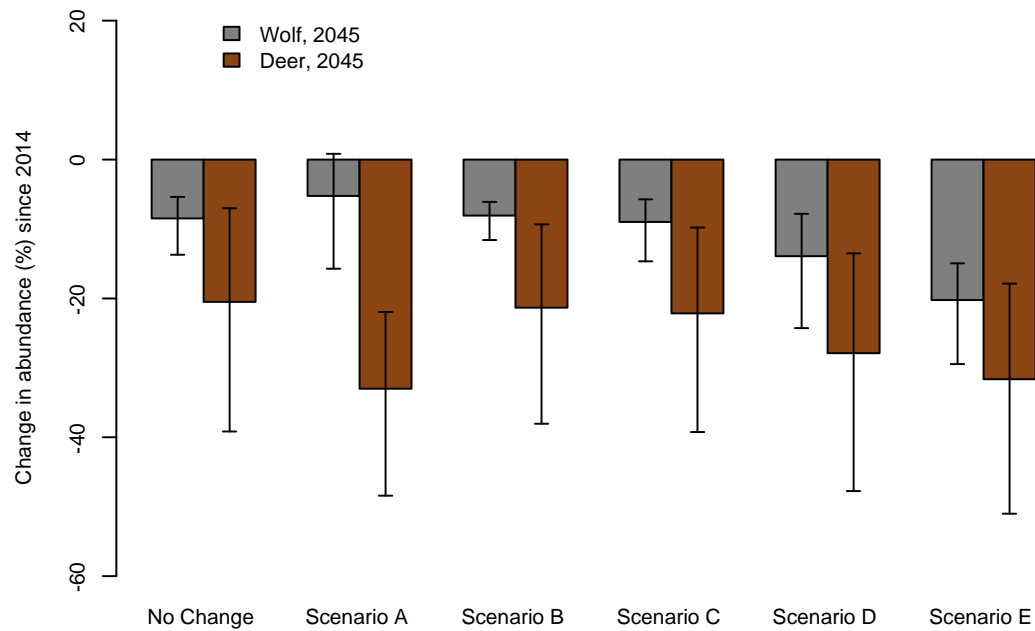


Figure 7. Sensitivity of wolf and deer abundance to a) vegetation change, b) road decommissioning, c) winter severity frequency, d) wolf diet composition, and e) hunting of deer by humans. Abundance is shown as percent change from 2014-2045 in wolf (grey) and deer (brown) abundance with 95 % confidence interval bars.

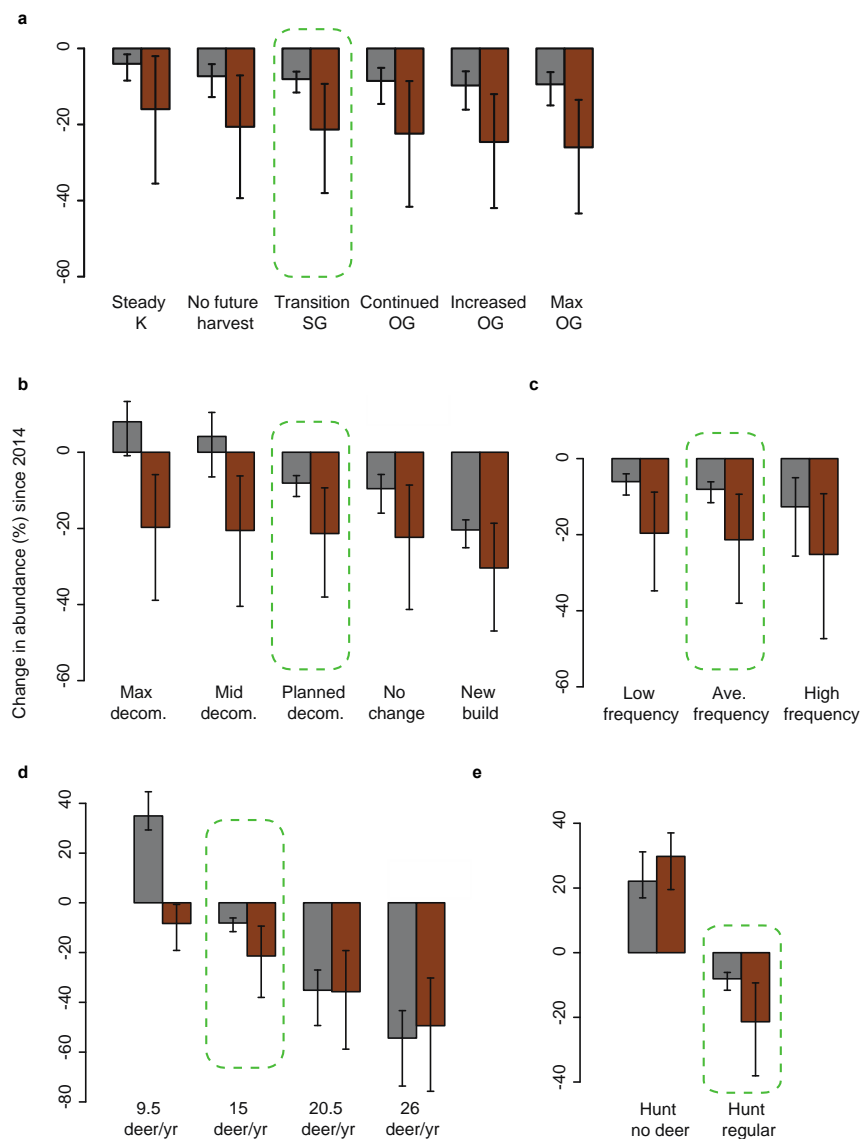


Figure 8. Sensitivity of wolf and deer abundance to wolf harvest regulation given a) planned decommissioning of roads, and b) maximum decommissioning of roads. Wolf harvest conditions shown are 0% reported harvest (i.e., harvest closure, but unreported harvest continued), 20 % cap on reported harvest, and 30 % cap on reported harvest. Abundance is shown as percent change from 2014-2045 for wolves (grey) and deer (brown) with 95 % confidence interval bars.

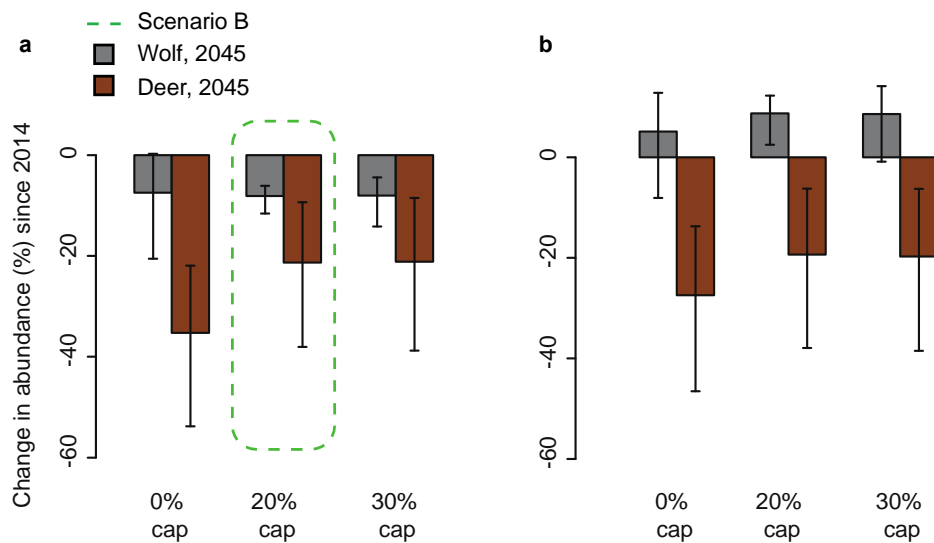
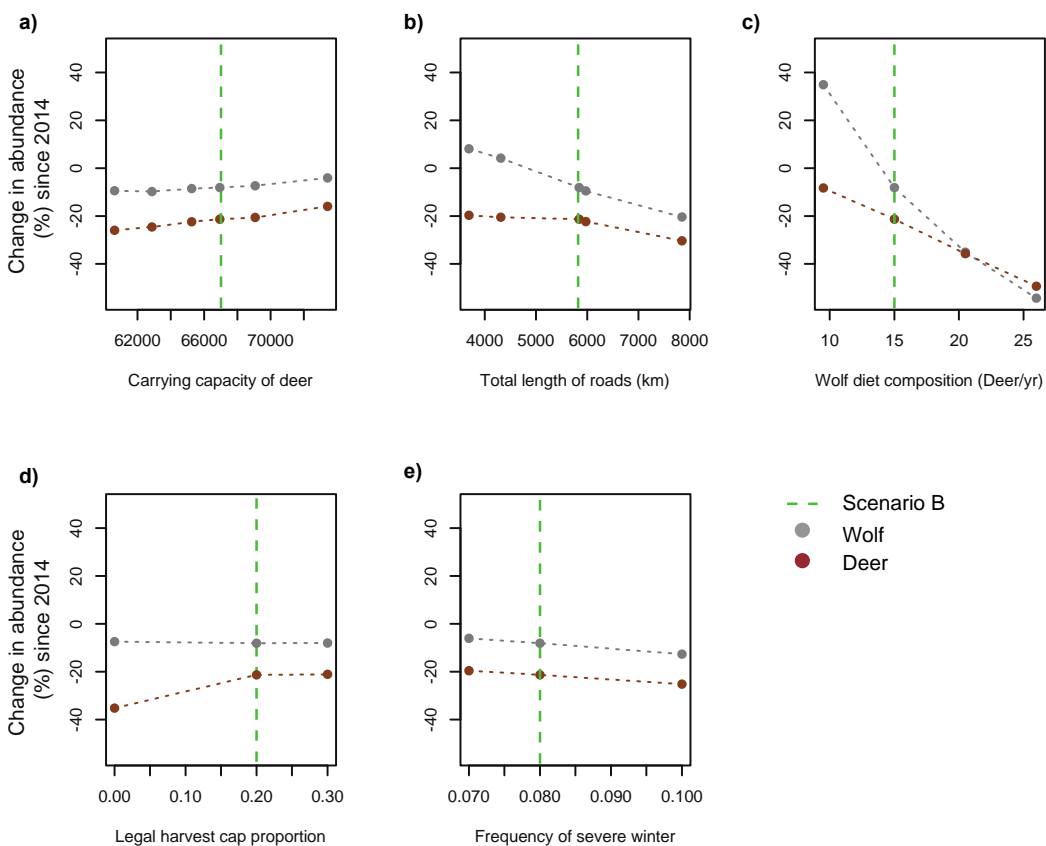


Figure 9. Change in wolf (grey points) and deer (brown points) in response to perturbations in a) vegetation, translated to deer carrying capacity, b) road length in the study area, c) wolf diet composition, d) regulation of reported wolf harvest, and e) frequency of severe winters. The green line indicates conditions of Scenario B for each variable.



APPENDIX A

Description of model parameters and equations, including differences from the Person (2001) model, where applicable.

Deer model

The deer model we construct is not sex or age-structured, and includes only an adult segment of the population with characteristic survival and reproductive rates (i.e., all deer were considered to be equally vulnerable to mortality causes, and sex ratio was effectively 1:1). Person (2001) also employed this model structure, after exploring sex- and age-structured models and finding no difference in model performance or outcomes (Person 2001, p. 54). We assume density-dependence recruitment, which we approximate using a theta-logistic function. Density dependence in deer has not been specifically quantified in this ecosystem, and as a result, we retain this relationship from Person (2001). However, we add predation by black bears of fawns and adults based on recent work on deer ecology conducted on Prince of Wales Island (Person et al. 2009, Gilbert 2015). The parameters of the deer model describe U_t , the deer population in spring (prior to the annual birth pulse). The deer population at time t is calculated across pack areas as $U_t = \sum_{i=1}^j U_{t(i)}$, where j is the number of wolf packs. For each pack area i , the deer population at time t is calculated as:

$$U_{t+1(i)} = U_{t(i)} + R_{ut(i)} - BA_{t(i)} - CP_{at(i)} - H_{t(i)} \quad (1)$$

Where $R_{ut(i)}$ is recruitment into the deer population, $BA_{t(i)}$ is predation mortality of adult deer by black bears, $CP_{at(i)}$ is predation mortality of deer by wolves, and $H_{t(i)}$ is death from human hunting. C , the per-capita wolf predation rate (26 deer/year/wolf) in the original model was based

on scat analysis and we updated this rate to 15 deer/year/wolf based on stable isotope analysis (Szepanski et al. 1999). $P_{at(i)}$ is the average of spring and fall population sizes of wolves in year t .

Recruitment into the deer population is described as:

$$R_{ut(i)} = U_{t(i)} r_{max} \left[1 - \left(\frac{U_{t(i)}}{K_{t(i)}} \right)^\theta \right] - BF_{t(i)} \quad (2)$$

Where $R_{ut(i)}$ is recruitment in pack area i at time t , r_{max} is the maximum per capita rate of increase in the absence of predation and hunting, θ is the density dependence parameter, $K_{t(i)}$ is the carrying capacity of deer in pack area i at time t , and $BF_{t(i)}$ is predation of fawns by black bears. In addition, severe winters with deep snow are known to strongly impact deer populations in Southeast Alaska (Person et al. 2009, Gilbert 2015), primarily through reduced fawn survival. Consequently, we included a binomial parameter for winter severity, the derivation of which is described in more detail in subsequent sections. While adult deer can die during extremely severe winters, we chose to include the effects of severe winters on deer by reducing recruitment to zero if a severe winter occurred. This is a relatively optimistic assumption from the standpoint of deer abundance, as while recruitment is unlikely to be truly zero (Gilbert 2015), adult deer also die during severe winters in reality (Klein and Olson 1960, Kirchhoff 1994, Person et al. 2009), while we do not include any adult deer mortality due to severe winters.

We assumed that bear predation of fawns was partially compensatory, so that as population density relative to K increased, proportion of bear predation that is compensatory increased, up to a maximum of 50% compensation. We used the following relationships to modify the base mortality rate of 0.46 ($SD= 0.023$) by deer density:

$$\text{If } \left[1 - \left(\frac{U_{t(i)}}{K_{t(i)}} \right) \right] < 0.5, \quad \text{then } BF_{t(i)} = 0.5 * 0.46 \quad (3)$$

$$\text{If } \left[1 - \left(\frac{U_{t(i)}}{K_{t(i)}} \right) \right] \geq 0.5, \quad \text{then } BF_{t(i)} = \left[1 - \left(\frac{U_{t(i)}}{K_{t(i)}} \right) \right] * 0.46$$

In contrast, we assumed predation of black bears on adult deer, as well as predation by wolves and death due to human hunting, were completely additive (Gasaway et al. 1992, Hayes et al. 2003), and thus constant despite changes in deer density. While it has been suggested that wolf predation on ungulates may follow a Type II functional response curve (Dale et al. 1994), no published relationships exists for a functional response curve between deer density and wolf predation. In addition, such a functional response would likely have a large effect on deer only at very low deer densities (Dale et al. 1994). As a result, we treat wolf predation as a constant, density-independent rate, allowing us to simplify the model. In addition, we calculated predation by black bears on adults, $B_{t(i)}$, as a rate of 0.03 ($SD = 0.0015$) based on analysis of combined deer mortality data from Person et al. (2009) and Gilbert (2015), following methods described in Gilbert (2015).

Predation mortality of deer by wolves, $CP_{at(i)}$, is the product of the average number of deer killed per wolf per year (C), and $P_{at(i)}$, the average number of wolves in pack i during year t ($P_{at(i)}$). $P_{at(i)}$ is calculated as the average (a) of the spring and fall wolf populations, $\left(P_{t(i)} + (P_{t(i)} + R_{t(i)}) \right) / 2$, where $P_{t(i)}$ is the spring wolf population in pack area i and year t , and $R_{t(i)}$ is reproduction in pack i in year t .

Deaths of deer due to human hunting, $H_{t(i)}$, was represented as:

$$H_{t(i)} = (U_{t(i)} + R_{t(i)}) * h * (1 + \beta_d * Km\ Roads) \quad (4)$$

where h is the base rate of harvest when roads are absent and β_d is a coefficient representing the additional harvest of deer by hunters with an increase in road access. The values of h and β_d were taken from the published regression relationship in Person (2001, Page 80), based on harvest and road-length data from Prince of Wales Island. Specifically, Person and Bowyer (1997) derived a baseline hunting rate, h , of 0.012, and regression relationships for additional risk in the presence of roads that was dependent on road length:

$$H_{t(i)} = h * (1 + 0.038 * Km\ roads) \quad (5)$$

Deer carrying capacity, $K_{t(i)}$, depends on habitat in pack area i at time t , and is a product both of the underlying productivity of the area (i.e., what original old-growth forest types existed in the area), and of subsequent timing and extent of timber harvest. Following timber harvest, forage changes in predictable ways through stages of forest succession (Alaback 1982), and as a result carrying capacity of deer changes as well (Hanley and Rogers 1989). The relationship between old-growth and second-growth forest types and deer carrying capacity is described in the model using the Deer Habitat Suitability Index (HSI), a system developed by management agencies in Southeast Alaska to evaluate the effects of management decisions on deer (Suring et al. 1993). We chose to use the deer HSI as a metric of deer carrying capacity because it is the management standard in the region and is integrated into a GIS framework, and has yet to be replaced by a better solution. Deer abundance was initiated at 0.75 of K in 1995.

Winter severity

In the model, deer recruitment, as mentioned above, depends on winter severity. Person (2001) treated winter severity as a random binomial variable based on temperature and precipitation data from the National Weather Service on Annette Island and Sitka, and data from Alaska Department of Fish and Game (unpublished data, Person 2001). This resulted in an average of 6 severe winters per century.

We re-analyzed the definition of a severe winter with deer recruitment of zero using precipitation data from Annette Island. We defined a severe winter as one in which total snowfall is >160 cm and maximum monthly snow depth is >25 cm. Parker et al. (1999) found that when maximum snow depths were >29.6 cm energy costs associated with movement of an average-sized deer (25–30 cm carpus height) increased significantly. During the first winter, fawns weigh ~40% less than adults (Parker et al. 1999) and their carpus height is ~10% shorter than for adults (Parker et al. 1984); thus, maximum snow depth of 25 cm should account for fawn energy expenditure with locomotion. For context, most forbs are covered when snow depths >10 cm (Parker et al. 1999).

Applying the proposed definition, 2 winters of 20 between 1995 and 2014 qualify as being “severe” (2000–2002, 2008–2009; Table 1). This rate of 10% is higher than that used by Person 2001; 2 severe winters from 1947 to 1996), but is somewhat comparable with his estimate of 6 severe winters in a century (6%).

We applied % change in snowpack provided by Littell (2015) to predict future snow conditions on POW; this was done as a rate ($2/20=0.10$). Littell (2015) predicted future snow between 2030

and 2059 using 5 different global climate models (GCM; Table A1); percent change ranges between 0 and -28.6% with a 5-GCM average of -19.2%.

Table A1. Historical, projected future, and projected percent change in precipitation as snow for Prince of Wales Island, Alaska based on five Global Climate Models (GCM; data from Littell 2015).

Climate conditions	Precipitation as snow (mm)	Change (%)
Historical (1970–1999)	453.3	--
GCM Projections (2030–2059 A2 emissions)		
UKMOHadCM3	453.3	0
CCCMA-CGCM3.1 t47	353.2	-22.1
MIROC3.2 medres	344.1	-24.1
GFDL-CM2.1	356.9	-21.3
MPI-ECHAM5	323.5	-28.6
5-GCM average	366.2	-19.2

Predicted low frequency (-28.6% change in snow fall) = 0.07 (0.10 rate X 0.714). Predicted average frequency (19.2% change) = 0.08 (0.10 rate X 0.808). Predicted high frequency (0% change) = 0.10. These rates were applied for the 2015-2045 probability of a severe winter depending on the scenario conditions.

Wolf Model

The wolf model is similar in structure to the deer model, with a non-age or –sex structured population of adult wolves and a density dependent annual reproductive output. In general, the wolf population takes the form:

$$P_{t+1(i)} = P_{t(i)} + R_{pt(i)} - T_{t(i)} - D_{t(i)} - M_{t(i)} + I_{t(i)} \quad (6)$$

Where $P_{t+1(i)}$ is spring pack size prior to parturition for wolf pack in area i . The initial pack size was random with a mean equal to 6.

$R_{pt(i)}$ is recruitment to pack i and equaled:

$$R_{pt(i)} = b \left[1 - \frac{CP_{t(i)}}{\alpha U_{t-2(i)}} \right] \quad (7)$$

in the original model, where b is average litter size when ratio of prey:wolves is very high (i.e.,

$\frac{CP_{t(i)}}{\alpha U_{t-2(i)}}$ approaches 0), and α is proportion of deer population available to the pack in area i . Note

that deer abundance is indexed to year $t-2$, which creates a 2-year lagged response of wolves to deer. Proportion of deer available was a random variable between 0.5-1.0. Average litter size was updated from 6 (SD = 0.3) to 4.1 (SD = 1.7) based on Person et al. (2009). Also litter size was capped at 11 based on the recommendations from Alaska Department of Fish and Game Region I.

$T_{t(i)}$ is the number for wolves harvested from pack i . We used actual, reported wolf harvest for 1995-2013 multiplied by a scalar for unreported harvest (31/18) based on Person and Russell (2008) and D. Person (pers. comm.).

Wolf harvest (harvest rate, HR) for 2014-2045 was a function of road density and distance from shoreline to nearest community since access to wolves was dependent on vehicles and boats (Person and Russell 2008, Table 6) and HR (wolves harvest/100 km²) was different for road densities >0.9km/km²:

$$\text{If road density} \leq 0.9; HR_{t(i)} = [0.073 + 1.126(\text{road density})]^2 \quad (8)$$

$$\text{If road density} > 0.9; HR_{t(i)} = [0.952 - 0.009(\text{ocean distance})]^2.$$

HR was converted to number of wolves harvested based on the size of the pack area and then multiplied by the unreported harvest scalar. These relationships were established by Person and Russell (2008), and were based on data on legal reported harvest of wolves on Prince of Wales from 1990-1998. As Person and Russell discuss, newer wolf harvest data were not included, because patterns of reporting of legal harvest changed after an emergency closure of harvest in 2001, while patterns of mortality in radio-collared wolves did not.

Number of dispersers from a pack in area i was a function of pack size and the predator:prey ratio:

$$D_{t(i)} = (P_{t(i)} + R_{pt(i)} - T_{t(i)}) \left[d \left(\frac{CP_{t(i)}}{\alpha U_{t-2(i)}} \right) \right] \quad (9)$$

with a base dispersal rate (d) of 0.5 (SD = 0.3). We updated disperser annual survival probability to 0.34 (SD = 0.3) based on Person and Russell (2008) and we allowed the disperser pool to carry forward each year, which was not the case in the original model. These updates resulted in fewer unoccupied pack areas and pack areas unoccupied for a shorter period of time. These changes addressed concerns expressed at the March workshop about the lack of the ability of packs to expand into unoccupied areas.

Number of wolves dying in pack area i in year t was a function of number of wolves in the area and the predator:prey ratio:

$$M_{t(i)} = (P_{t(i)} + R_{t(i)} - T_{t(i)} - D_{t(i)}) \left[m \left(\frac{CP_{t(i)}}{\alpha U_{t-2(i)}} \right) \right] \quad (10)$$

with a base mortality rate (m) of 0.5 (SD = 0.3).

Immigration into a pack area ($I_{t(i)}$, 1 or 2 wolves) occurred if the pack area was occupied by <2 wolves, there were dispersers available to disperse from any pack area, and the predator:prey ratio ($\frac{CP_{t(i)}}{\propto U_t}$) >2 , which represented sufficient prey to support a wolf pair. Unoccupied pack areas received 2 wolves when these conditions were met and those with 1 wolf received a single immigrant.

APPENDIX B

Methods used for estimation of vegetation conditions across a range of management scenarios to support application of the Interagency Deer Habitat Suitability Model.

To estimate the changes in vegetation in the study area due to 6 different possible timber harvest management decisions, we used the following assumptions to construct GIS-based maps of vegetation change at 10-year intervals (i.e., in 2015, 2025, 2035, and 204). These vegetation changes were subsequently used to calculate changes in deer carrying capacity. For each vegetation scenario, we discuss assumptions by land designation such as likely amount of harvest of different forest classes, and include the Mental Health Land Trust Exchange Proposal (MHLT), the Sealaska Land Entitlement Finalization, Tongass National Forest lands, State of Alaska Forest lands, and Other ANCSA Corporation lands.

1) No future harvest

This potential vegetation future assumes no further harvest of timber in the Prince of Wales study area after 2014, including no harvest of lands that are part of Mental Health Land Trust Exchange Proposal, the Sealaska Land Entitlement Finalization, Tongass National Forest lands, State of Alaska Forest lands, and Other ANCSA Corporation lands.

2) Transition to young growth

This potential vegetation future is based on the transition from harvest of old-growth to young-growth forest, as planned by the U.S. Forest Service, and includes some harvest of old growth to

supply the timber industry over a 10-15 year period while more young-growth grows to harvestable age.

Tongass National Forest

- The land base excludes roadless areas according to 2001 Roadless Rule, and is located entirely within the 2008 Tongass Land Management Plan (USFS 2008) Phase 1 Suitable Land Base.
- Assumes the Big Thorne Timber Sale proceeds, and provides an estimated 149 million board feet (mmbf) of old-growth (OG) timber.
- The location and schedule of additional OG and young-growth (YG) projects are those currently described in the 5-year schedule of activities. These include small OG sales as part of Kosciusko Island Stewardship (12 mmbf YG, 1 mmbf OG) in 2015; Naukati-Staney-Sea Otter Sound (10 mmbf YG, 10 mmbf OG) in 2017; Polk Inlet/12-Mile Stewardship (20 mmbf YG, 10 mmbf OG) in 2018, Neck Lake/Alder Creek (13 mmbf OG) in 2019, and Polk/12-Mile Stewardship II (5 mmbf YG, 5 mmbf OG) in 2018.
- Specific locations of YG units to be logged in 2nd-rotation, even-aged harvest during this period were provided by USFS, and total approximately 40,000 acres.
- For OG harvest, the specific locations of timber stands to be logged were identified by first limiting the query to the specific watersheds (Value Comparison Units) listed in the USFS Activities Schedule. This land base contains more than enough timber to meet this level of demand. A sub-set of timber lands most likely to be logged was identified using a timber Resource Selection Function (RSF) developed by Albert and Scheon (2013) based on stand characteristics disproportionately selected for logging during 1954 – 2004. We refer to these

stands as ‘preferentially selected’ timber lands, as distinct from the more general classification of ‘suitable’ used in the TLMP. We adjusted the resource selection index to meet the required volume estimates of each sale, equivalent to $RSF > 0.5$ and yielding an estimated 1,195 acres of OG harvest and a total of approximately 40.5 mmbf of sawlog + utility (S + U) volume.

Mental Health Land Trust Exchange Proposal

- Assumes that the MHLT exchange is not approved.

Sealaska Land Entitlement Finalization

- Includes lands transferred to Sealaska under the Land Entitlement Finalization Act of 2014.
- These lands contain approximately 33,228 acres of productive OG forest, with approximately 25,422 acres of preferentially selected ($RSF > 0.18$) OG timber lands containing approximately 842 mmbf of OG timber (S+U).
- Assumes that preferentially selected OG timber within these lands would be logged at an even rate over 30 years for an average rate of approximately 850 acres or 28 mmbf/year.

State of Alaska forest lands

- Includes logging expected to continue on State Forest Lands.
- The State of Alaska State Forest manages approximately 48,472 acres in the Southeast Alaska State Forest, with approximately 28,500 acres of these in the Prince of Wales study area. These lands contain an estimated 10,954 acres of preferentially selected ($RSF > 0.18$) OG timber lands and 333.3 mmbf of timber.

- Assumes that preferentially selected OG timber lands managed by the State of Alaska will be logged at an even pace over the 30 year period (2015 – 2045) of 365 acres or 11 mmbf /year.

Other ANCSA Corporation lands

- Accounts for logging expected to continue on lands currently owned by ANCSA village and regional corporations. Not including the Sealaska Land Finalization Act, ANCSA corporations own approximately 326,683 acres within the Prince of Wales study area. These lands currently contain approximately 161,000 acres of previously logged forest lands and an estimated 97,600 acres remaining in OG condition.
- Because of this relatively high level of previous harvest, and under the assumption that most of the originally economic timber lands have already been harvested, we applied a more conservative estimate of potential future logging on ANCSA corporation lands using a selectivity index of RSF >40 to estimate OG timber remaining that will potentially be logged in the future. Using this assumption, we estimate approximately 13,000 acres of productive OG timber available for future harvest on ANCSA corporation lands.
- Assumes these preferentially selected timber lands will be logged at an even pace over the 30 year period, with approximately 434 acres or 14 mmbf logged per year (Table A1).

3) Continued harvest of old-growth forest

This potential vegetation future is the result of the continued harvest of old-growth forest at observed recent levels (2008-2014).

Tongass National Forest

- The land base excludes roadless areas according to 2001 Roadless Rule, and is located entirely within the TLMP 2008 Phase 1 Suitable Land Base.
- Assumes approximately 34 mmbf per year of timber (S + U) from the Tongass National Forest. The proportion of supply from POW is assumed to be 37% of total Tongass supply, or 12.6 mmbf/year, 126 mmbf/decade or 377 mmbf during 2015 – 2045 (Table A1). This is based on proportional representation of all Tongass timber that occurs within Prince of Wales suitable, roaded and Phase 1 land base.
- Assume Big Thorne Timber Sale proceeds, and accounts for a proportion of the demand described above. The estimated 149 mmbf from Big Thorne would reduce the remaining demand for OG supply from POW to a total of 228 mmbf during the period 2015-2045.
- Uses an RSF > 0.67 provided approximately the correct number of acres to meet this scenarios assumption.

Mental Health Land Trust Exchange Proposal

- Assumes that the MHLT exchange is approved.
- Preferentially selected (RSF > 0.18) OG forest lands within the MHLT exchange parcels include 13,952 acres and approximately 488.7 million board-feet of timber (S + U).
- Assumes that preferentially selected OG timber within these lands would be logged at an even rate over 30 years for an average rate of 462 acres or 15 mmbf/year (Table A1).

Sealaska Land Entitlement Finalization

- Accounts for lands transferred to Sealaska under the Land Entitlement Finalization Act of 2014.
- These lands contain approximately 33,228 acres of productive OG forest, with approximately 25,422 acres of preferentially selected ($RSF > 0.18$) OG timber lands containing approximately 842 mmbf of OG timber (S + U).
- Assumes that preferentially selected OG timber within these lands would be logged at an even rate over 30 years for an average rate of approximately 850 acres or 28 mmbf/year.

State of Alaska Forest Lands

- Accounts for logging expected to continue on State Forest Lands.
- The State of Alaska State Forest manages approximately 48,472 acres in the Southeast Alaska State Forest, with approximately 28,500 acres of these in the Prince of Wales study area. These lands contain an estimated 10,954 acres of preferentially selected ($RSF > 0.18$) OG timber land and 333.3 mmbf of timber (SL + U).
- Assumes that preferentially selected OG timber lands managed by the State of Alaska will be logged at an even pace over the 30 year period (2015 – 2045) of 365 acres or 11 mmbf/year.

Other ANCSA Corporation Lands

- Accounts for logging expected to continue on lands currently owned by ANCSA village and regional corporations, including approximately 326,683 acres within the Prince of Wales study area. These lands currently contain approximately 161,000 acres of previously logged forest lands and an estimated 97,600 acres remaining in OG condition.

- Because of this relatively high level of previous harvest, and under the assumption that most of the originally economic timber lands have already been harvested, we applied a more conservative estimate of potential future logging on ANCSA corporation lands using a selectivity index of RSF >40 to estimate OG timber remaining that will potentially be logged in the future. Using this assumption, we estimate approximately 13,000 acres of productive OG timber available for future harvest on ANCSA corporation lands.
- Assumes these preferentially selected timber lands will be logged at an even pace over the 30 year period, with approximately 434 acres or 14 mmbf logged per year (Table A1).

4) Increased harvest of old-growth forest

This potential vegetation future is the result of increased harvest of old-growth forest at observed former levels (1995-2000).

Tongass National Forest

- The land base excludes roadless areas according to 2001 Roadless Rule, and is located entirely within the TLMP 2008 Suitable Land Base of all phases (1, 2 & 3) of the TLMP Adaptive Management Strategy.
- Assumed Supply from POW is 35.5% of total Tongass supply, or 47.6 mmbf/year, 476 mmbf/decade or 1,427 mmbf during 2015 – 2045. This is based on proportional representation of all Tongass timber that occurs within the Prince of Wales suitable, roaded and Phase 1,2 & 3 land base.
- Assume Big Thorne Timber Sale proceeds, and accounts for a proportion of the supply demand described above. In this case, the estimated 149 mmbf from Big Thorne would

reduce the remaining demand for OG supply from POW to a total of 1,278 mmbf during the period 2015 – 2045.

Mental Health Land Trust Exchange Proposal

- Assumes that the MHLT exchange is approved.
- Assumes that preferentially selected OG timber within these lands would be logged at an even rate over 15 years for an average rate of 923 acres or 30 mmbf/year (Table A1).

Sealaska Land Entitlement Finalization

- Accounts for lands transferred to Sealaska under the Land Entitlement Finalization Act of 2014.
- Assumes that preferentially selected OG timber within these lands would be logged at an even rate over 15 years for an average rate of approximately 1,700 acres or 56 mmbf/year (Table A1).

State of Alaska Forest Lands

- Accounts for logging expected to continue on State Forest Lands.
- Assumes that preferentially selected OG timber lands managed by the State of Alaska will be logged at an even pace over the 15 year period (2015-2030) of 730 acres or 22 mmbf/year.

Other ANCSA Corporation Lands

- This scenario assumes preferentially selected timber lands ($RSF > 0.4$) currently owned by ANCSA corporations (not including Sealaska Land Finalization) will be logged at an even pace over the 15 year period of 2015-2030, with approximately 868 acres or 28 mmbf logged per year (Table A1).

5) Maximum harvest of old-growth forest

This potential vegetation future is the result of the maximum harvest of old-growth forest at highest levels described in the TLMP (all lands/Phase 1-3/intensive).

Tongass National Forest

- Assumes maximum harvest allowable under the 2008 TLMP, or approximately 267 mmbf/year from the entire Tongass National Forest.
- Assumes that administrative protections applied under the Roadless Rule is repealed for the Tongass National Forest. The land base for this scenario includes roaded and roadless areas within the TLMP 2008 Suitable Land Base of all phases (1, 2 & 3) of the TLMP Adaptive Management Strategy.
- Assumed Supply from POW is 25.5% of total Tongass supply, or 69.2 mmbf/year, 692 mmbf/decade or 2,074 mmbf during 2015-2045. This is based on proportional representation of all Tongass timber that occurs within the Prince of Wales suitable and available land base under the 2008 TLMP.
- Assumes Big Thorne Timber Sale proceeds, and accounts for a proportion of the supply demand described above. The estimated 149 mmbf from Big Thorne would reduce the

remaining demand for OG supply from POW to a total of 1,925 mmbf during the period 2015-2045.

Mental Health Land Trust Exchange Proposal

- Assumes that the MHLT exchange is approved.
- Assumes that preferentially selected OG timber within these lands would be logged at an even rate over 10 years for an average rate of 1,385 acres or 45 mmbf/year (Table A1).

Sealaska Land Entitlement Finalization

- Accounts for lands transferred to Sealaska under the Land Entitlement Finalization Act of 2014.
- Assumes that preferentially selected OG timber within these lands would be logged at an even rate over 10 years for an average rate of approximately 2,500 acres or 84 mmbf/year (Table A1).

State of Alaska Forest Lands

- Accounts for logging expected to continue on State Forest Lands.
- Assumes that preferentially selected OG timber lands managed by the State of Alaska will be logged at an even pace over the 10 year period (2015-2030) of 1,100 acres or 33 mmbf/year.

Other ANCSA Corporation Lands

- Assumes preferentially selected timber lands ($RSF > 0.4$) currently owned by ANCSA corporations (not including Sealaska Land Finalization) will be logged at an even pace over the 10 year period of 2015- 2030, with approximately 1,300 acres or 42 mmbf logged per year (Table A1).

Table A1: Summary of assumptions for rate of harvest of old-growth (OG) and young-growth (YG) across categories of land ownership in the Prince of Wales study area among future vegetation changes considered. Land ownership designations include Tongass National Forest lands (TNF), the Sealaska Land Entitlement Finalization (SL), the Metal Health Land Trust Exchange Proposal (MHLT), State of Alaska Forest lands (SAF), and Other ANCSA Corporation lands (AC).

Vegetation	TNF	SL	MHLT	SAF	AC	Total
<i>Transition to YG</i>	USFS 5-yr Schedule of Activities.	30 yrs, 28 mmbf/yr	Remains TNF	30 yrs, 11 mmbf/yr	30 yrs, 14 mmbf/yr	53 mmbf/yr + Transition Schedule
<i>Continued OG</i>	12.6 mmbf/yr	30 yrs, 28 mmbf/yr	30 yrs, 15 mmbf/yr	30 yrs, 11 mmbf/yr	30 yrs, 14 mmbf/yr	80.6 mmbf/yr
<i>Increased OG</i>	47.6 mmbf/yr	15 yrs, 56 mmbf/yr	15 yrs, 30 mmbf/yr	15 yrs, 22 mmbf/yr	15 yrs, 28 mmbf/yr	183.6 mmbf/yr
<i>Maximum OG</i>	69.2 mmbf/yr	10 yrs, 84 mmbf/yr	10 yrs, 45 mmbf/yr	10 yrs, 33 mmbf/yr	10 yrs, 42 mmbf/yr	273.2 mmbf/yr